

BULLETIN
of **CARNEGIE MUSEUM OF NATURAL HISTORY**

**ARIKAREEAN, HEMINGFORDIAN, AND
BARSTOVIAN MAMMALS FROM THE MIOCENE
COLTER FORMATION, JACKSON HOLE,
TETON COUNTY, WYOMING**

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ABSTRACT

Miocene mammal faunas of three different land-mammal ages are superposed in the Colter Formation of Jackson Hole, Wyoming. The late-early Arikareean (=ca. 23–25 mya) Emerald Lake Fauna most closely resembles those of the upper half of the *Meniscomys* Concurrent-range Zone and includes the new apodontid *Allomys cristabrevis*, new species, and the new leporid *Archaeolagus emeraldensis*, new species. The East Pilgrim Assemblage is composed of fossils from at least two, and maybe three, stratigraphically separate localities. The stratigraphically highest local fauna in the Assemblage is one of the few of early Hemingfordian age (ca. 18–19 mya) known from the Montana-Wyoming Rockies. It shares species with faunas of the Runningwater Formation in Nebraska. However, the stratigraphically lowest oredont in the East Pilgrim Assemblage is referred to *Merychyus arenarum*, a species that is common in the late Arikareean Marsland Formation (=Hunt's, 1985, Upper Harrison beds). Both the Emerald Lake Fauna and the East Pilgrim Assemblage are found in andesitic, trachytic, and latitic tuffaceous rocks probably indicative of compressional-type volcanism and

tectonism. The Cunningham Hill Fauna, containing the first late Barstovian (=ca. 12–14 mya) small mammals described from Wyoming, correlates with the *Copemys longidens* or *Copemys russelli* Assemblage Zones of the Barstow Formation; it includes the new species *Oreolagus colteri*, new species (ochotonid), *Lignimus transversus*, new species, and *Mojavemys magnumarcus*, new species (geomyids). The Cunningham Hill Fauna also yields the first northern Rocky Mountain records for *Petauristodon*, *Diprionomys agrarius*, *Lignimus*, *Mojavemys*, *Copemys kelloggae*, and *Schaubeumys*. The Cunningham Hill Fauna occurs in rhyolitic tuffaceous rocks usually associated with extensional volcano-tectonic regimes. All of the Colter faunas show greater affinity with Great Plains faunas than with those west of the Rockies. The Arikareean and Barstovian faunas are composed of suites of species that differ from similarly aged assemblages of the Great Plains and Far West, apparently because ecological conditions were different. The suite of species in the Cunningham Hill Fauna provides evidence that the terms "early Valentinian" and "late Barstovian" refer to overlapping intervals of geologic time.

INTRODUCTION

Fossil mammals from the Colter Formation of Jackson Hole, northwestern Wyoming, occur in an intermontane basin of both geological and paleontological interest. The geological interest stems from the remarkably thick Tertiary section—some 12 km with rocks of every epoch—of which the Colter comprises a significant part (1,500 m). Such thick deposits are uncommon in intermontane basins of the northern Rocky Mountains, and record a complex history of Tertiary volcanism and tectonism in Jackson Hole (Barnosky, 1983, 1984; Behrendt et al., 1968; Love et al., 1973, 1978; and references therein). The fossil mammals are important in dating the tectonic events and in providing a geographic link between well known faunas of the Far West (=Oregon, California, Nevada) and the Great Plains. This report analyzes three distinct faunas of Miocene mammals from the Colter Formation, describes five new species, dates a probable change from compressional to extensional-type volcanism in north-

western Wyoming, and discusses interregional relationships between faunas of the northern Rocky Mountains, the Far West, and the Great Plains. The geology of the Colter Formation in particular and Jackson Hole in general is reported separately (Barnosky, 1983, 1984; Love and Reed, 1971; Love et al., 1973).

The youngest fauna, of late Barstovian age, is the most diverse and is the first record for small mammals of this age in Wyoming. Only two other Barstovian occurrences of small mammals have been published for the northern Rockies, the Anceney fauna of Gallatin County (Dorr, 1956) and the Flint Creek fauna of Granite County, Montana (Black, 1961). Both of the published faunas are small, although Sutton (1977) in an unpublished doctoral dissertation showed a greater diversity at Anceney. The Hemingfordian and Arikareean faunas from Jackson Hole, while sparsely represented, provide the only Rocky Mountain records for some taxa.

LIST OF ABBREVIATIONS

AMNH—American Museum of Natural History. AUG—Augustana College. CMNH—Carnegie Museum of Natural History. F:AM—Frick Collection, American Museum of Natural History. FMNH—Chicago Field Museum of Natural History. LACM—Los Angeles County Museum of Natural History. KUV—Uni-

versity of Kansas Museum of Natural History. ROM—Royal Ontario Museum. SDSM—South Dakota School of Mines and Technology, Museum of Geology. UCMP—University of California Museum of Paleontology. UMMP—University of Michigan Museum of Paleontology. UNSM—University of Nebraska

State Museum. UO—University of Oregon Museum of Natural History. USGS—United States Geological Survey. USNM—Smithsonian Institution, United States National Museum. UWBM—Thomas Burke Memorial Washington State Museum, University of Washington. UWYO—University of Wyoming

Museum of Geology. YPM—Yale Peabody Museum. AP—longest anteroposterior diameter. T—widest transverse diameter. TA—widest transverse diameter, anterior half of tooth. TP—widest transverse diameter, posterior half of tooth. my(a)—million years (ago).

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specimens. Additional types and material were graciously loaned by Craig C. Black (material from CMNH), Mary R. Dawson (CMNH), John F. Sutton (material from CMNH), Larry D. Martin (KUVP), David P. Whistler (LACM), Gordon Edmund (ROM), Philip D. Gingerich (UMMP), and Robert J. Emry (USNM). I thank Bob Wood and Charles McCurdy (Acting Chief Naturalists) of Grand Teton National Park; John Wilbrecht (Director), Kevin Ryan and John Decker (Assistant Managers), Jim Griffin (Outdoor Recreation Manager) of the National Elk Refuge; and District Rangers Garth Baxter (Hoback), Mac Murdock (Black Rock), Paul DeMeule and Joe Kinsella (Gros Ventre) of the U.S. Forest Service for granting permission to work on lands under their jurisdiction. The project was carried out in conjunction with the USGS, by which funds were partially provided. Additional financial support was contributed by the National Science Foundation (Grant EAR-8110865), the Geological Society of America, Sigma Xi, the Corporation Fund of the University of Washington Department of Geological Sciences, and the Leverhulme Foundation.

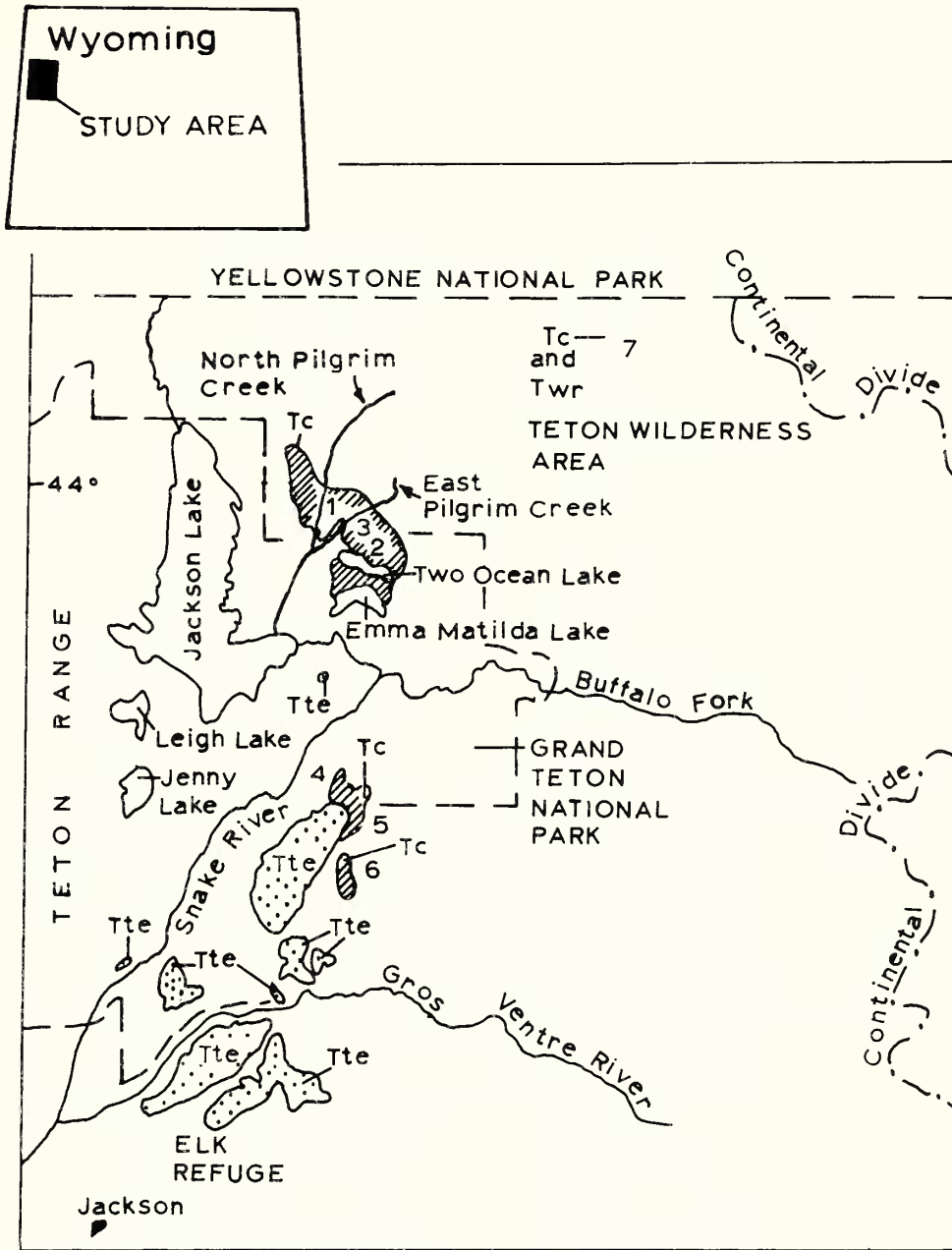
GEOLOGIC SUMMARY OF COLTER FORMATION

The Colter Formation, a complexly bedded sequence of volcanoclastics, is confined to Teton County, Wyoming, and mostly to Jackson Hole (Figs. 1 to 3). All exposures crop out along streams and slide scarps and most are within or adjacent to Grand Teton National Park. Measured sections summarized in Figs. 4 to 8 and described in detail by Barnosky (1983, 1984) show that at least 70 distinct beds are superposed to form the Colter and can be broadly grouped into two very distinctive members.

The Crater Tuff-breccia Member composes the bottom third of the formation, Units 1 through 34, and is characterized by interbedded tuffs and tuff-breccias of andesitic, trachytic, and latitic composition. It is confined to the area around Pilgrim Creek, Two Ocean Lake, and Emerald Lake. Distinctive features in outcrop include (1) gray to very bright green color and (2) abundant angular tuff-breccias that seldom include quartz cobbles. Chemically, the rocks can be distinguished by a relatively low SiO₂ content (less than 72% recalculated water-free). In contrast, the overlying Pilgrim Conglomerate Member, Units 35 through 70, is composed of conglomerate, sandstone, and claystone, as well as tuff and

tuff-breccia. The member is rhyolitic and further differentiated from rocks in the lower member by (1) pink, tan, green, blue-gray, or white color and (2) frequent occurrence of rounded quartzite cobbles within conglomerates that are made mostly of angular to sub-rounded volcanic rocks. Chemically, SiO₂ contents above 72% characterize tuffs in the Pilgrim Conglomerate Member, which crops out near Pilgrim Creek, Two Ocean Lake, Cunningham Hill, Shadow Mountain, and Ditch Creek. The mid-Tertiary unconformity (Fields et al., 1985; Rasmussen, 1973; Thompson et al., 1982; and references therein) apparently coincides with the abrupt contact between the two members, and may be represented by the unconformable contact of the upper member with Paleocene rocks on Shadow Mountain. Faults (Fig. 2) cause repetition of Units 2 through 19 along East Pilgrim Creek (Fig. 4), and of most of the Pilgrim Creek section (Figs. 4, 5) along Two Ocean Lake (Fig. 7).

Near-vent facies of ignimbrite and coarse tephra show that both members accumulated on and near the flanks of volcanoes that were active in northwestern Jackson Hole through much of the early



after Love, 1956; Love et al, 1976

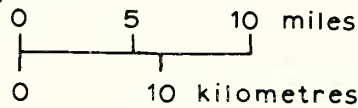


Fig. 1.—Geographic index map. Numbers show geographic areas mentioned in text. 1—Pilgrim Creek, 2—Two Ocean Lake, 3—Crater Mountain, 4—Cunningham Hill, 5—Shadow Mountain, 6—Ditch Creek, 7—Emerald Lake.

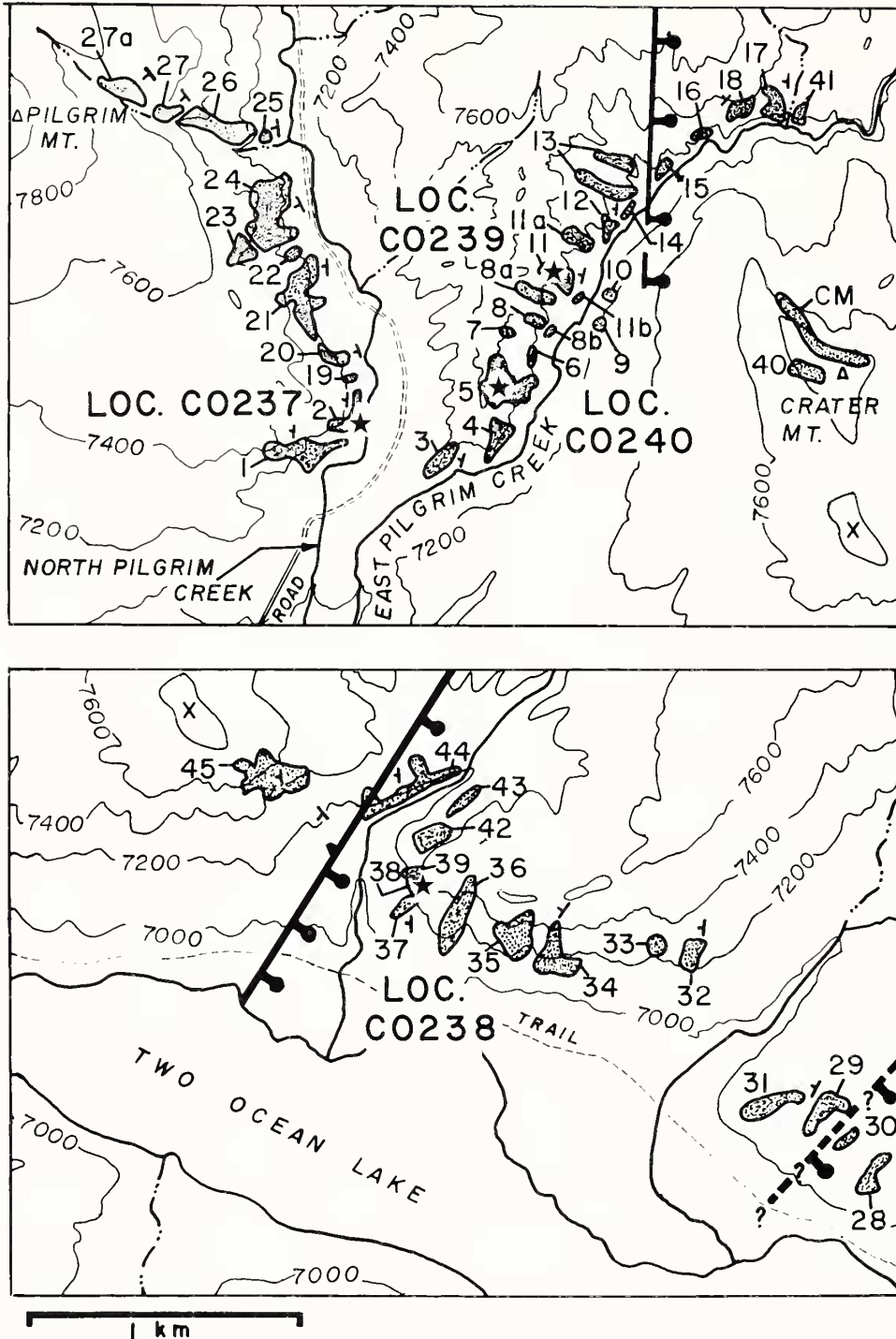


Fig. 2.—Detail maps. *Top*: Region around Pilgrim Creek (Area 1 in Fig. 1) and Crater Mountain (Area 3). *Bottom*: Region around Two Ocean Lake (Area 2). Numbers identify stippled outcrops that were prospected and through which sections were measured. Topographic base is redrafted from part of Two Ocean Lake 7.5' Quad. X's show where upper and lower maps overlap. Stars indicate UWB fossil vertebrate localities. Heavy black lines show major faults; dots on short bars mark downthrown block. Contour interval 200 ft. North at top.

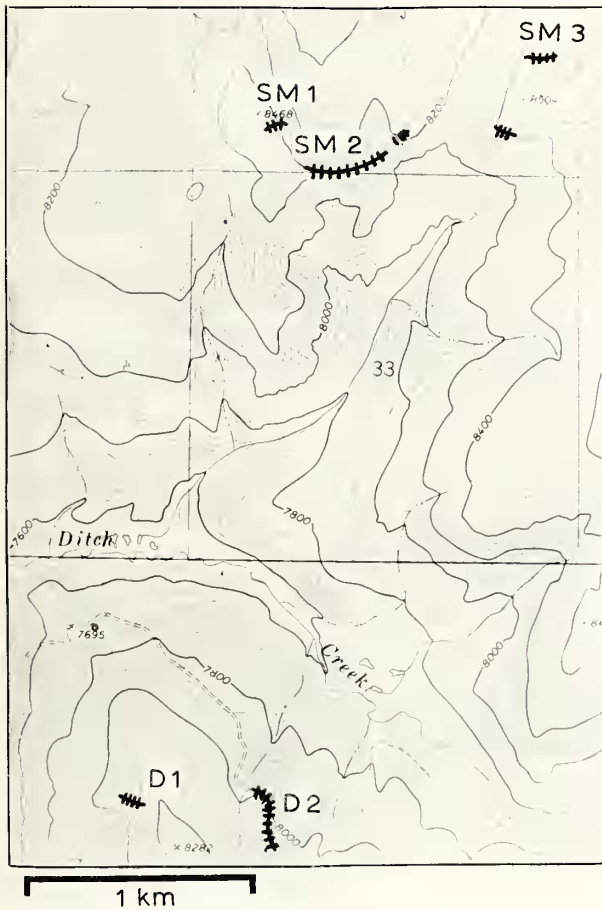
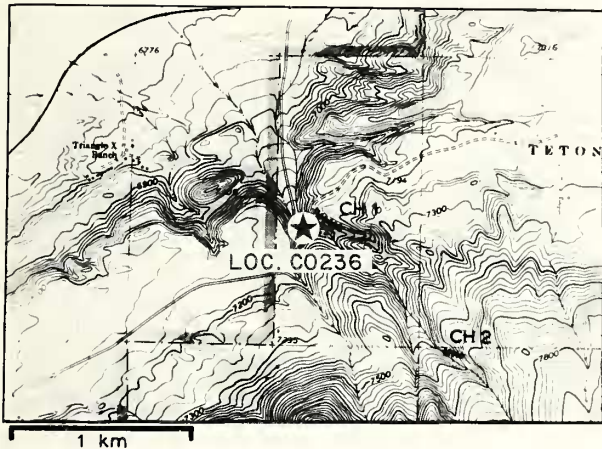


Fig. 3.—Detail maps. *Top*: Cunningham Hill (Area 4 on Fig. 1). Base is part of Moran 7.5' Quad. *Bottom*: Shadow Mountain (SM) and Ditch Creek (D) (Areas 5 and 6). Base is part of Shadow Mountain 7.5' Quad. Heavy lines with cross bars identify outcrops that were prospected and through which sections were measured. Stars indicate UWBM fossil vertebrate localities. Contour interval 40 ft. North at top.

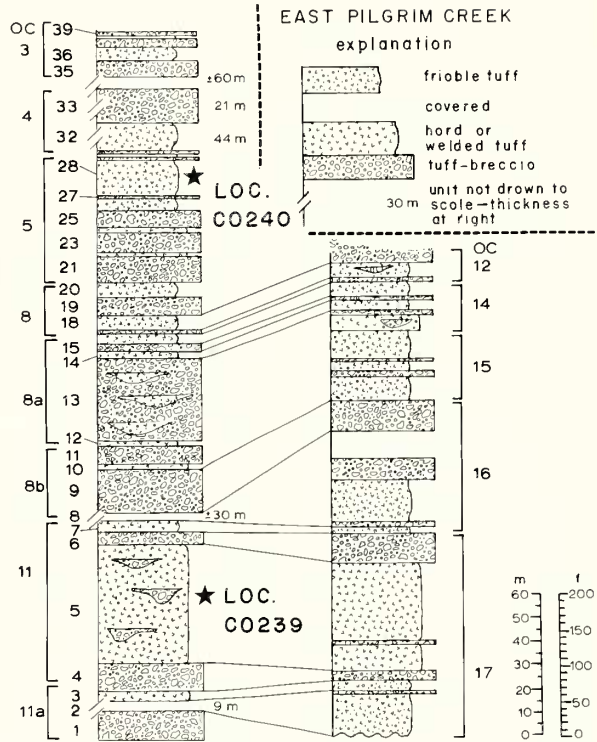


Fig. 4.—Lower third of the type section of the Colter Formation, measured along East Pilgrim Creek (Area 1 on Fig. 1). Numbers to the left of the section identify lithologic units. Brackets denote outcrops (OC) through which units were measured. Numbers outside the brackets label outcrops, which correspond to those shown on Fig. 2. Stars indicate UWBM fossil vertebrate localities.

and middle Miocene (Barnosky, 1983, 1984). The Colter Formation thus represents the only volcanic center known to be active in northwest Wyoming-southwest Montana between 20 and 8 my ago (Chadwick, 1981). The andesitic, trachytic, and latitic tuffs in the lower member suggest that volcanism was associated with compressive tectonics, whereas rhyolitic tuffs in the upper member are characteristic of volcanic activity in an extensional regime (Lipman et al., 1972; Christiansen and Lipman, 1972). The formation therefore apparently records the Mid-Tertiary change from compressional to extensional tectonics that took place throughout the western U.S. (Stewart, 1978; Christiansen and Lipman, 1972; Lipman et al., 1972), and provides an opportunity for more precisely dating the change in the Montana-Wyoming region. At present, fossil mammals give the only reliable dates for the Colter Formation. Problems with excess argon in glass shards and allogenic sanidine crystals have complicated attempts at K-Ar age determinations.

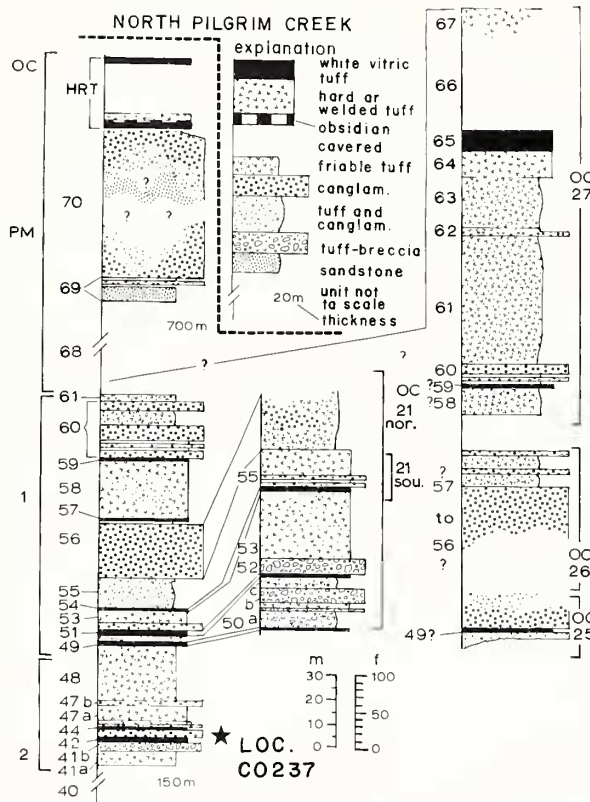


Fig. 5.—Upper two thirds of type section of the Colter Formation, measured along North Pilgrim Creek (Area 1 on Fig. 1). Star indicates UWBM fossil vertebrate locality. See Fig. 4 for further explanation.

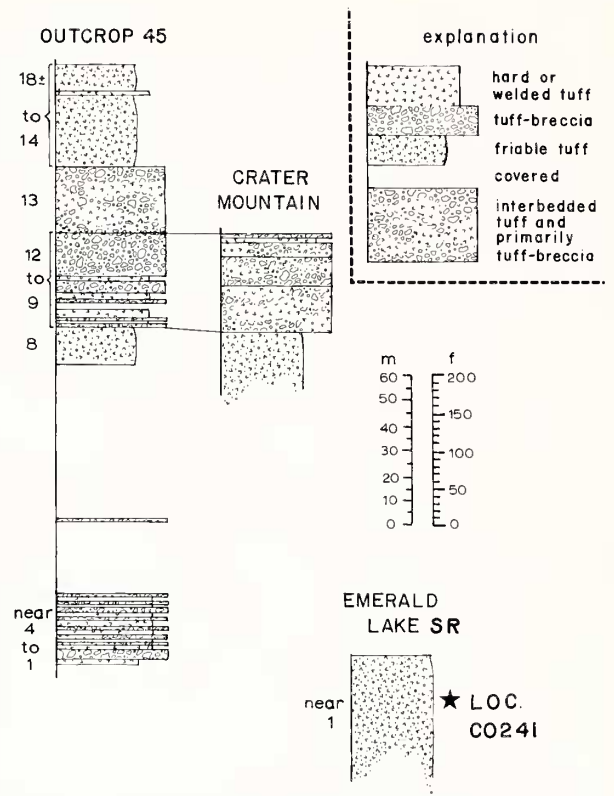


Fig. 6.—Stratigraphic sections at Outcrop 45 (Area 2 on Fig. 1), Crater Mountain (Area 3), and Emerald Lake (Area 7). Unit numbers correspond to those in Fig. 4, where further explanation is given. Star indicates UWBM fossil vertebrate locality.

HISTORY OF PALEONTOLOGICAL INVESTIGATIONS

In the late 1930's a local cowboy, Roy Saunders, reported the first vertebrate fossils from Jackson Hole. The bones were *in situ* along East Pilgrim Creek somewhere between Units 5 and 28, and included the skull of an oreodont (*Merychylus*) and foot bones of the camel *Oxydactylus* (Colbert, 1943; Schultz and Falkenbach, 1947). Subsequently, J. D. Love began detailed geologic investigations in the area and found the East Pilgrim 5 (UWBM loc. C0240) and Cunningham Hill (UWBM loc. C0236) localities. By the late 1960's, his continued efforts along with those of C. C. Black, M. R. Dawson, and M. C. McKenna had produced small faunas from Cunningham Hill (UWBM loc. C0236), Emerald Lake (UWBM loc. C0241), and East Pilgrim 5 (UWBM loc. C0240). In 1968, enough material existed for Black to suggest a Hemingfordian age for the East Pilgrim 5 and Cunningham Hill assemblages, which agreed with earlier interpretations by

Love (1956). With continued collecting by J. F. Sutton, it became apparent that strata at Cunningham Hill were somewhat younger, perhaps Barstovian in age (Sutton and Black, 1972). Sutton and Black also concluded that the East Pilgrim 5 assemblage resembled faunas of the Runningwater Formation (late-early Hemingfordian). Later, Love et al. (1976) determined the age of the Emerald Lake locality to nearly equate with that of the Monroe Creek Formation (late-early Arikarean), and Sutton and Black (1975) described Chadronian mammals from below the Colter Formation (OC 41 of Fig. 2). Most of the reports on Colter fossils were based on fragmentary specimens that commonly were few in number. Therefore in 1978, at the suggestion of Love, work culminating in this report began in order to more precisely determine the taxonomic, biostratigraphic, and biogeographic affinities of the mammals from the Colter Formation.

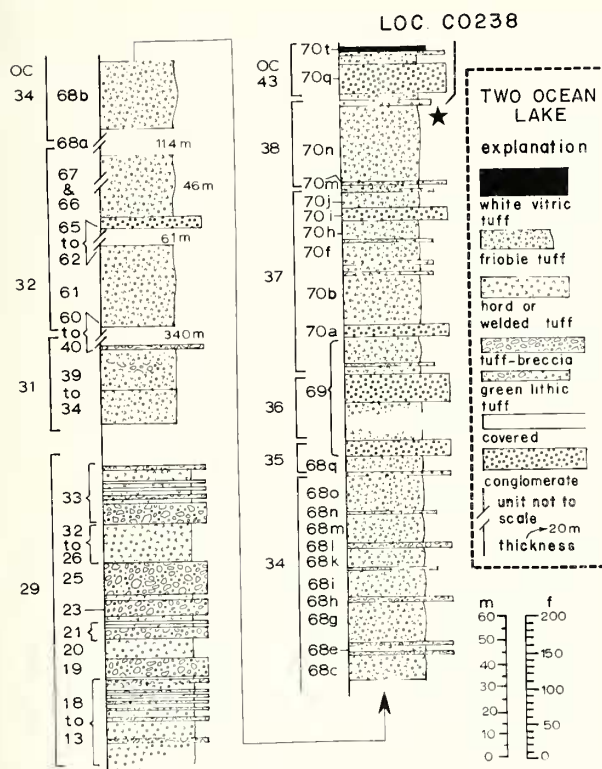


Fig. 7.—Stratigraphic section along north shore of Two Ocean Lake (Area 2 on Fig. 1). Unit numbers correspond to those in Figs. 4 and 5, where further explanation is given. Star indicates UWBM fossil vertebrate locality.

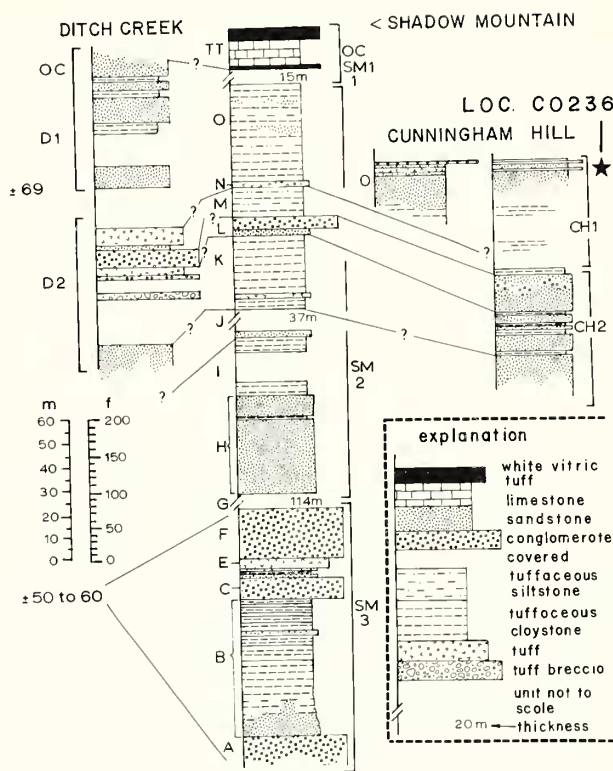


Fig. 8.—Stratigraphic section through Ditch Creek (Area 6 on Fig. 1), Shadow Mountain (Area 5), and Cunningham Hill (Area 4). Outcrops through which the sections were measured are mapped on Fig. 3. Capital letters designate units where lenticularity of beds, geographic separation, and different facies prevent direct correlation to type section; ± numbers at left indicate approximate match to type section. Star indicates UWBM fossil vertebrate locality.

METHODS

FIELD

Outcrops of the Colter Formation within the heavily-vegetated study area were located from air photos, 7.5' orthophotos, and 7.5' geologic maps (Love, 1973 and unpublished data) corresponding to the Two Ocean Lake, 1968, Moran, 1968, Shadow Mountain, 1968, and Mount Hancock, 1959, USGS topographic map quadrangles. Each outcrop mapped on Figs. 2, 3, and in Love et al. (1976:fig. 3) was systematically searched at approximately 2-m contour intervals to locate flakes of fossil bone at least 2 mm in size. Where bone occurred, enough matrix to fill at least one burlap feed bag (about 100 lbs or 45 kilos) was washed through screens containing 16 squares per 1 inch (about 12 squares per 1 cm). Resulting concentrate was dried and searched in the field without magnification and was deemed rich enough for additional collecting with recovery of one or more identifiable cheek teeth per 45 kilos of unwashed matrix. The only two sites rich enough were North Pilgrim 2 (UWBM loc. C0237) and Cunningham Hill (UWBM loc. C0236), from which totals of 2,585 kilos (about 5,700 lbs) and 3,120 kilos (6,875 lbs) of matrix, respectively, were washed. After drying in the field, concentrate was sorted into size fractions by shaking it through a series of

five nested, spring-mounted screens with mesh sizes of 4, 8, 16, 20, and 30 squares per inch. The 4 and 8 mesh fractions were searched and discarded in the field. Concentrate finer than 30 mesh was not searched. Large bones were collected by standard plaster bandaging techniques when necessary.

To place fossils within the proper stratigraphic context, detailed sections were measured through each outcrop and could usually be correlated with the continuous type section along Pilgrim Creek by marker beds, lithologic similarities, or superpositional relationships. For each of the sections, each lithologically distinct stratum was considered a Unit for which thickness to the nearest decimeter, rock type, grain size, roundness, sphericity, cementation, composition, color, sorting, bedding, sedimentary structures, fossils, orientation of paleocurrent indicators, and strike and dip were determined. Faults were recognized by detailed repetition of units in association with slickensides and extremely fractured rock.

LABORATORY

The 16 mesh concentrate was generally searched under a 1.5× illuminated magnifier and smaller size fractions under an 8×

binocular microscope. Ninety-two identifiable teeth were recovered from the Cunningham Hill concentrate, and 162 from North Pilgrim 2. Measurements smaller than 5 mm were taken through a grid-reticule mounted on the ocular of a Nikon binocular microscope at $31\times$. Dial calipers were used for measurements between 5 mm and 140 mm, and a mm rule for those over 140 mm. Unless otherwise noted, all anteroposterior and transverse measurements of teeth are maxima (not necessarily at the occlusal surface) and the transverse measurement was taken perpendicular to the anteroposterior one. For geomyoid teeth, maxima in occlusal view did not differ significantly from maxima taken in side and posterior views.

All published specimens were examined except for Saunders' material, which is well illustrated in Colbert (1943) and Schultz and Falkenbach (1947). In the systematics, the use of "cf." denotes tentative referral to a species. The use of "near" denotes a species that cannot be definitely determined with the material at hand, is morphologically most similar to a given form, but shows some characters suggestive of a new species. When the material warrants only generic identity, the name of the genus is followed by "species indeterminate."

Radiometric dates have been corrected by the IUGS constants listed in Dalrymple (1979) unless noted otherwise.

FOSSIL OCCURRENCES

Although fossil mammals are generally scarce in the Colter Formation, they fortuitously occur near the bottom and top of each member (Table 1). In the lower member unit 1SR (UWBM loc. C0241), Unit 5 (UWBM loc. C0239), and Unit 28 (UWBM loc. C0240) have yielded fossils. Unit 1SR (Fig. 6) lies at the base and Unit 28 (Fig. 4) is near the top of the member; these two units approximately bracket the part of the Colter formed by compressional-type volcanism. The upper member produced fossils from Unit 43 (UWBM loc. C0237), Unit O (UWBM loc. C0236), and Unit 70o (UWBM loc. C0238). The assemblage from Unit 43 (Fig. 5) is near the base of the upper member and provides a minimum age for the inception of extensional-type volcanism. The Unit O assemblage (Fig. 8) probably occurs in the upper third of the upper member.

Fossils are superposed in the type section along East and North Pilgrim Creeks. The fossiliferous Unit 1SR, although cropping out some 30 km to the northeast near Emerald Lake (Fig. 1, Area 7), correlates with beds near Unit 1 in the type section on the basis of lithologic similarities. Tuff of both areas is massive, gray, fine grained, vitric, and friable to moderately indurated in most exposures. Unit O at Cunningham Hill apparently correlates with strata near Unit 69 in the type and Two Ocean Lake sections, because only in these areas are bluish rocks, yellow-green sandstones with pumice chunks, laminated whitish-tan tuff, and tan conglomerate found interbedded. Localities that have yielded only one taxon each occur in Unit 5 of the East Pilgrim section (Fig. 4) and Unit 70o of the Two Ocean Lake section (Fig. 7). Precise geographic positions of the fossil localities are as follows.

Cunningham Hill, UWBM loc. C0236. —

43°45.7'N, 110°33.31'W, NE ¼ of SE ¼ Sec. 20, T. 44 N, R. 114 W, Teton County, Wyoming, Moran 7.5' Quad, 1968. In Unit O, Pilgrim Conglomerate Member of Colter Formation.

North Pilgrim 2, UWBM loc. C0237. — 43°55.81'N, 110°33.63'W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake 7.5' Quad, 1968. In Unit 43, Pilgrim Conglomerate Member of Colter Formation.

Two Ocean Lake, UWBM loc. C0238. — 43°55.25'N, 110°31.57'W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake 7.5' Quad, 1968. In Unit 70o, Pilgrim Conglomerate Member of Colter Formation.

East Pilgrim 11, UWBM loc. C0239. — 43°56.30'N, 110°33.00'W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake 7.5' Quad, 1968. In Unit 5, Crater Tuff-Breccia Member of Colter Formation.

East Pilgrim 5, UWBM loc. C0240. — 43°55.92'N, 110°33.23'W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake Quad, 1968. In Unit 28, Crater Tuff-Breccia Member of Colter Formation.

Emerald Lake SR, UWBM loc. C0241. — 44°05.33'N, 110°18.90'W, unsurveyed, NW ¼ Sec. 33, T. 48 N, R. 112 W, Forest Service arbitrary grid, Teton National Forest Map, 1966, 15,400 feet (4,084 m) SSW of milepost 29 on south boundary of Yellowstone Park, Teton County, Wyoming, Mount Hancock 15', 1959. Near Unit 1, Crater Tuff-breccia Member of Colter Formation.

The bones accumulated in three different depositional environments (Barnosky, 1983, 1984). Cunningham Hill (Unit O; UWBM loc. C0236) and North Pilgrim 2 (Unit 43; UWBM loc. C0237) represent portions of Miocene stream channels where pebble

Table 1.—Fossil localities in the Colter Formation.

Locality name	Locality number	Synonyms	Stratigraphic position (oldest at bottom)
<i>Pilgrim Conglomerate Member</i>			
Two Ocean Lake	UWBM loc. CO238	None	Unit 70o
Cunningham Hill	UWBM loc. CO236	KUVP loc. WYO 84	Unit O (=±69)
North Pilgrim 2	UWBM loc. CO237	None	Unit 43
<i>Crater Tuff-Breccia Member</i>			
East Pilgrim 5	UWBM loc. CO240	USNM—"S. Fork Pilgrim Creek, 5 mi. N. of Moran" KUVP loc. WYO 86 CMNH—"East Fork of Pilgrim Creek"	Unit 28
Roy Saunders Locality	None	None	Between Unit 5 and 28?
East Pilgrim 11	UWBM loc. CO239	None	Unit 5
Emerald Lake 1 SR	UWBM loc. CO241	AMNH—"SR near Emerald Lake on Fox Creek."	near Unit 1

sized bones and teeth were concentrated by currents. At Cunningham Hill, all material comes from a lense measuring about 2 m wide by 1 m deep (Pl. I, top). At North Pilgrim 2, fossils weather from a small scarp about 1 m wide by 3 m high (Pl. I, bottom). Most material came from slope wash at the base of

these two localities. Fossils at East Pilgrim 5 (Unit 28; UWBM loc. CO240) and Two Ocean Lake (Unit 70o; UWBM loc. CO238) were preserved by volcanic ash falls. Bones at East Pilgrim 11 (Unit 5; UWBM loc. CO239) were incorporated into the base of an ash-flow.

SYSTEMATIC PALEONTOLOGY

Order Insectivora Illinger, 1811

Family Talpidae Fischer von Waldheim, 1817

Subfamily Talpinae Fischer von Waldheim, 1817

Tribe Scalopini Dobson, 1883

Genus *Domninoidea* Green, 1956

Domninoidea sp., cf. *D. storeri* Russell, 1976

Plate II A,B

Locality.—North Pilgrim 2, UWBM loc. CO237.

Age.—Late Barstovian.

Range of genus.—Fig. 9.

Referred specimen.—M₃, UWBM 62728.

Measurements.—AP = 1.8 mm. TA = 1.2 mm. TP = 0.9 mm.

Description and comparison.—Terminology of talpid teeth follows that illustrated in Barnosky (1981:figs. 4, 6). UWBM 62728, an M₃, is referred to *Domninoidea* on the bases of relatively small size and lingually open talonid basin (Pl. II A, B). UWBM 62728 shares these characters with the genotypic species, *D. riparensis* Green, 1956, and with all other species of the genus (Fig. 9). A wide anterior cingulum, characteristic of *Domninoidea*, was apparently present on UWBM 62728 but has been broken.

UWBM 62728 differs from *Domninoidea storeri* (Russell, 1976) only in slightly smaller size (0.3 mm shorter AP). Both show a small metastylid, which is absent in the smaller *D. riparensis* (AP = 1.5 mm) (Green, 1956:153–154). *D. valentinensis* (Reed, 1962:3) possesses a considerably larger M₃ (AP = 2.6 mm), as does *D. mimicus* (AP = 2.61–3.13 mm, Wilson 1968:108; Freeman, 1979:8). M₃'s have not been reported from Barstow or Quartz Basin.

M₃'s are larger in *Scalopus mcgrewi* (AP = 2.95–3.15 mm) (Voorhies, 1977:133), *Scapanus* (AP near 2 mm), *Proscalops tertius* (AP = 1.99–2.63 mm) (Bjork, 1975:810), *Proscalops secundus* (AP = near 2.1 mm), and *Proscalops evelynae* (AP = 2.2 mm) (MacDonald, 1963:169; Barnosky, 1982:1105). M₃ in *Oligoscalops* is smaller (AP = 1.5 mm) (Reed, 1961:475). *Neurotrichus* differs from UWBM 62728 in possessing a wider talonid neck. *Gaillardia* is distinct from UWBM 62728 in lacking connection between the metastylid and the metaconid (Hutchison, 1968:48).

Discussion.—UWBM 62728 cannot be differentiated from M₃'s of *D. storeri*. In view of the meager record of *Domninoidea*, however, referral to *D. storeri* is tentative.

RANGE OF *DOMNINOIDES*

● TYPE LOCALITY

FAUNA FM	BARSTOW " "	QUARTZ B. BUTTE CR. VS. MALHEUR & LAKE CO., OR	NIOBRARA R. VALENTINE CHERRY CO., NB	BURGE VALENTINE KEYAPAPA CO., NB	WAKEENEY OGALLALA TREGO CO., KS	WOLF CREEK SHANNON CO., SD	KLEINF. FM WOOD MT. S. SASKATCH	CUNNINGHAM COLTER TETON CO., WY
LOCATION	SAN BERNADINO CO., CA							
HEMP-HILLIAN								
CLARENDONIAN	LATE				<i>D. mimicus</i> Wilson, 1968	<i>D. riparensis</i> Green, 1956		
	EARLY			<i>D. mimicus</i> Freeman, 1979				
BARSTOVIAN	LATE	<i>D. sp.</i> Lindsay, 1972	<i>D. sp.</i> Hutchison, 1968	<i>D. valentinensis</i> Reed, 1962			<i>D. storeri</i> Russell, 1976	<i>D. cf. D. storeri</i>

Fig. 9.—Geographic and stratigraphic range of *Domninoides*.

Genus *Scalopoides* Wilson, 1960

Scalopoides, species indeterminate

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Arikareean: Monroe Creek microfauna of Shannon County, South Dakota (MacDonald, 1972). Hemingfordian: Martin Canyon Quarry A of Logan County, Colorado (Wilson, 1960). Batesland fauna of Bennett County, South Dakota (Martin, 1976). Vedder fauna of Santa Barbara County, California (Hutchison and Lindsay, 1974). Late Barstovian: Quartz Basin, Red Basin faunas of Harney and Malheur Counties, Oregon (Hutchison, 1968). Kleinfelder Farm fauna of Saskatchewan (Storer, 1975). Late Clarendonian: Black Butte Fauna of Malheur County, Oregon (Hutchison, 1968).

Referred specimen.—M₃, UWBM 62829.

Measurement.—AP = 1.9 mm. TA = 1.2 mm. TP = 0.9 mm.

Description and comparison.—In size and general morphology UWBM 62829 resembles *Scalopoides ripafodiator* and *S. isodens* (Hutchison, 1968). A comparison to *Scapanoscapter* and *Achlyoscapter* is impossible because unworn M₃'s of these genera are unknown. Unlike UWBM 62829, the metastylid and metaconid lack connection in *Gaillardia*. *Domninoides* differs from UWBM 62829 in lacking closure of the talonid basin. M₃ of *Mystipterus* is smaller (seldom exceeding 1.47 mm) than UWBM 62829, and additionally differs in having a basal cingulid. In *Neurotrichus*, the talonid is wider at the junction with the trigonid, in contrast to the narrow junction in the M₃ from Jackson Hole. M₃'s with a less prominent metacristid than that in UWBM 62829 characterize *Scapanus*. In *Scalopus mcgrewi* the tooth is

larger (AP = 2.95–3.15 mm) than the Jackson Hole specimen. M₃'s smaller than UWBM 62829 occur in *Oligoscalops* (AP = 1.5 mm). *Proscalops* and *Domninoides* differ from UWBM 62829 because the talonid opens lingually; the talonid basin is closed lingually in the Jackson Hole specimen. In *Mesoscalops* the tooth is more hyposodont than in UWBM 62829.

Scalopini, species indeterminate

Scalopoides, Sutton and Black, 1972.

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Referred specimens.—M¹, UWBM 62831. M₁ or M₂ fragment, KUVF 17489. M² fragment, KUVF 17488.

Description and comparison.—UWBM 62831 resembles the M¹ of *Achlyoscapter longirostris* (Hutchison, 1968:fig. 84) in size and general morphology. M¹ in *Scalopoides*, *Scapanoscapter*, and known *Domninoides* are larger (2.3 mm or more AP). *Scalopoides* further differs in possessing a well defined parastyle, in contrast to the small one in UWBM 62831. Specimens of *Scapanoscapter* (Hutchison, 1968:fig. 72) possess a more pronounced protoconule (=paraconule of Hutchison). The mesostyle in the Jackson Hole specimen closely resembles that of *Scalopoides*; the mesostyle is shorter in *Achlyoscapter*. Unlike the condition in *Mystipterus*, the posterior border of M¹ is not concave in any of these forms. UCMP 78774 from the Barstow Formation

RANGE OF *OREOLAGUS* ● TYPE LOCALITY

FAUNA	BEAUTY BUTTE	VIRGIN VALLEY	ANCENEY	QUARRY A	SPLIT ROCK	MARSLAND	CUNNINGHAM
FM	HARNEY	HUMBOLDT	MADISON V.	ARIKAREE	FREMONT	"	COLTER
LOCATION	CO., OR	CO., NV	GALLATIN	LOGAN CO., CO	CO., WY	DAWES CO., NB	TETON COWY
CLAREN- DONIAN							
BARSTOVIAN			<i>O. nevadensis</i> Sutton, 1977				<i>O. colteri</i> ● new species
	EARLY	<i>O. wallacei</i> ● Dawson, 1965	<i>O. nevadensis</i> ● Dice, 1917				
HEMING- FORDIAN				<i>O. wilsoni</i> ● Dawson, 1965	<i>O. nebrascen.</i> Dawson, 1965	<i>O. nebrascensis</i> ● McGrew, 1941	

Fig. 10.—Geographic and stratigraphic range of *Oreolagus*.

resembles the Jackson Hole specimen in general morphology but is larger (AP = about 2.8 mm).

KUVP 17488, a fragment of M², differs from that in *Scalopoides* in possessing a prominent metastyle located just anterior to the posterior margin of the tooth. The metastyle projects straight labiad. Like that in *Scalopoides isodens*, the mesostyle of KUVP 17488 shows no trace of division. The tooth is unknown in *Scapanoscapter* or *Achlyoscapter*. The mesostyle is divided in *Domninoidea*.

Order Lagomorpha Brandt, 1855
 Family Ochotonidae Thomas, 1897
 Genus *Oreolagus* Dice, 1917
Oreolagus colteri, new species
 Plate III A–H, J

Holotype.—UWBM 62698, P⁴ or M¹.

Hypodigm.—UWBM 62698, 62694, 62701, 62702, 62707, 62709, 62711 (P³), UWBM 62704, 62708, 62720, 62722, 62715 (P⁴ or M¹), UWBM 62714, 62717 (M²), UWBM 62718, 62719 (P₃), UWBM 62712, 62721 (P₄ or M₁).

Type locality.—North Pilgrim 2, UWBM loc. C0237.

Etymology.—For John Colter, an early trapper in Jackson Hole.

Age.—Late Barstovian.

Range of genus.—Fig. 10.

Referred specimens.—DP₃, UWBM 62697. DP₄, UWBM 62729. DP₂, UWBM 62815, 62817. Upper DP fragment, KUVP 17820. Lower molariform teeth, UWBM 62716, 62695, 62651, 62816. P⁴ or M¹, UWBM 62818.

UWBM 62815 through 62818 and KUVP 17820 from UWBM loc. C0236, others from type locality.

Diagnosis.—Small, with P³ seldom exceeding 2.4 mm wide, P⁴–M¹ usually less than 2.7 mm wide. P³ with anteroloph less than ½ width of tooth. P⁴–M¹ with prominent crescentic valley, hypostria not exceeding ¾ transverse width of tooth, two rudimentary root-bumps near occlusal surface labially. DP₃ with single groove bifurcating anterior surface of tooth. P₃ with lingual accessory groove sometimes present.

Description and comparison.—Cheek teeth from Jackson Hole match in all respects the generic characters of *Oreolagus* (Dawson, 1965:29), including absence of roots, and simplification of M² into a single, transversely elongate, basined column. The simplification implies loss of M³ although no palates were recovered. These characters differentiate *Oreolagus* from *Desmatolagus*, *Gripholagomys*, *Hesperolagomys*, *Russellagus*, and *Cuyamalagus*, in which M³, complexity in M², and roots are retained.

In the Jackson Hole species, the anteroloph of P³ (Pl. IIIF) reaches less than halfway across the tooth (Table 2), as in *O. wallacei* and the Anceney specimens referred to *O. nevadensis* by Sutton (1977). The anterolophs extend half the width of the premolar in *O. wilsoni* and *O. nebrascensis*. All of the Jackson Hole specimens are shorter anteroposteriorly than the single P³ of *O. wilsoni* reported by Dawson (1965:6, KUVP 10303, ratio AP/T = 0.61), and three of the six are more anteroposteriorly compressed relative to width (Table 2). Two specimens

Table 2.—Dental measurements, *Oreolagus colteri*, new species, Colter Formation.

Local-ity	Specimen	AP	Width antero-loph	T	AP/T
P ³					
NP	UWBM 62693	1.3	0.8	1.9	0.68
NP	UWBM 62694	1.3	1.0	2.4	0.54
NP	UWBM 62701	1.2	0.7	2.1	0.57
NP	UWBM 62707	1.3	1.1	2.3	0.57
NP	UWBM 62709	1.3	1.0	2.0	0.65
NP	UWBM 62711	1.2	0.8	1.8	0.67
AP Width hypo-stria T AP/T					
P ⁴ or M ¹					
NP	UWBM 62698	1.2	1.3	2.3	0.52
NP	UWBM 62704	1.5	1.2	2.7	0.56
NP	UWBM 62708	1.3	1.2	2.5	0.52
NP	UWBM 62720	1.4	1.4	2.2	0.64
CH	UWBM 62818	1.3	0.8	2.5	0.52
NP	UWBM 62715	1.5	0.8	—	—
NP	UWBM 62722	1.5	0.9	2.3	0.65
M ²					
NP	UWBM 62714	1.0	—	1.7	0.59
NP	UWBM 62717	1.0	—	1.9	0.53
AP TA TP					
P ₃					
NP	UWBM 62718	1.2	1.0	1.5	
NP	UWBM 62719	1.1	1.1	1.3	
P ₄ or M ₁					
NP	UWBM 62721	1.5*	1.8	1.7	
NP	UWBM 62712	1.8	1.7	—	
dP ₄					
NP	UWBM 62723	1.8	1.2	1.4	
dP ₃					
NP	UWBM 62697	—	—	1.4	
dP ²					
AP T					
CH	UWBM 62817	1.1		1.9	

* At least.
NP North Pilgrim 2.
CH Cunningham Hill.

of *O. nebrascensis* from Split Rock resemble *O. wilsoni* in these respects (CMNH 13750, UWYO 1952, AP/T = 0.61 and 0.63). P³ in *O. wallacei* is slightly larger and more anteroposteriorly compressed than the Jackson Hole material (AP/T = 0.51, LACM CIT 3074, Dawson, 1965:27). The P³'s from Anceney, CMNH 28533, 28538, 28686 (Sutton, 1977), resemble those of *Oreolagus* from Jackson Hole in size and fall within the range of anteroposterior compression (AP/T = 0.63, 0.68, 0.58). As in the other species, none of the P³'s of *O. colteri* show traces of roots.

The similarity of seven isolated teeth suggest that P⁴ and M¹ of *O. colteri* are nearly identical in occlusal morphology. Given an equal chance of preservation and recovery for P⁴ and M¹, the probability that any tooth is P⁴ is 0.50. Likewise, the probability that any tooth is M¹ is 0.50. The probability that all seven teeth are P⁴'s or all seven teeth are M¹'s is therefore $0.50^7 = 0.008$. Size differences should not bias the sample because these teeth are of similar dimensions in other species and relatively small M²'s and P₃'s were recovered.

A prominent crescentic valley characterizes all teeth from Jackson Hole (Pl. III A, G), but is lacking in M¹'s of *O. wallacei* and Sutton's sample from Anceney. Like *O. wilsoni*, the hypostria in the Jackson Hole teeth extends from $\frac{2}{5}$ to $\frac{3}{5}$ across the width of the tooth, which contrasts with that of M¹'s from Anceney, *O. nebrascensis*, and *O. wallacei* ($\frac{3}{4}$ to $\frac{4}{5}$). Judging from the usual condition in *Oreolagus*, teeth from Jackson Hole with a short hypostria (0.8–0.9 mm) are probably P⁴'s, whereas those with long ones (1.2–1.4 mm) most likely represent M¹'s. The hypostria persists throughout wear and, depending on wear-stage, short hypostria either abut the lingual edge of the crescentic valley (moderate wear) or terminate 1 to 3 mm from the valley (later wear stages). Long hypostria generally extend past the anterior part of the crescentic valley by about 1 mm (Pl. III A, B, G), except in the most advanced wear stages when they may stop as much as 0.2 mm short of the valley. Undescribed in any other species are two rudimentary root swellings that are homologous with roots of more primitive genera and occur labially near the occlusal surface (Pl. III D, E). In size, the P⁴'s and M¹'s are slightly smaller than in *O. wilsoni* (AP = 1.5–1.6 mm, T = 2.9 mm) and *O. wallacei* (AP = 1.6–1.7 mm, T = 2.7–2.8 mm) (Dawson, 1965), but resemble *O. nebrascensis* from Split Rock.

In general morphology, the worn M²'s of *O. colteri* (Pl. III H) closely approximate those of *O. wallacei* and *O. nebrascensis* from Split Rock. M²'s of *O. colteri* (Table 2) however, are smaller than in *O. wallacei*, most *O. nebrascensis*, and *O. wilsoni*, in which dimensions range from 1.0–1.2 mm AP and 2.1–2.3 mm T. The lingual fold is distinct in the Jackson Hole material, more like *O. nebrascensis* than *O. wallacei*.

One of the two P₃'s from Jackson Hole has a very shallow accessory lingual fold that is filled with cement. Such folds occur in *O. wilsoni* and *O. nebrascensis* but not in *O. nevadensis*. As is usual in *Oreolagus*, a short protoloph, long posterior loph,

and prominent labial groove characterize these teeth. Lower molariform teeth are fragmented and therefore cannot be differentiated from those of other species.

The DP² of *O. colteri*, with an extremely shallow hypostria that disappears when the tooth wears about half-way, possesses a prominent lingual root and a smaller labial one. The lingual root is squarer than in *O. wilsoni* but different wear-stages preclude other comparisons. The hypostria and lingual notch are slightly less pronounced in a figure of *O. nebrascensis* from Split Rock (FMNH PM2219, Dawson, 1965). A deciduous P₃ from Jackson Hole (Pl. III J), missing its posterior third, differs from that in *O. nebrascensis* and *O. wilsoni* in possessing a median groove on the anterior margin of the tooth, rather than a median lobe bordered on each side by grooves (see Dawson, 1965:fig. 28). Strong anterior and posterior roots occur on DP₄. The talonid is expanded more anteroposteriorly than the trigonid, but in *O. nebrascensis* from Split Rock the trigonid is more expanded.

Discussion.—*Oreolagus colteri* of Jackson Hole is relatively primitive in possession of rudimentary root-bumps on P⁴ and M¹ and apparent retention of crescentic valleys on M¹. Such features were previously known only in Hemingfordian species. *O. colteri* differs from these geologically older forms, however, in smaller size, configuration of DP₃, and short anteroloph on P³. It shares the short anteroloph on P³ with all Barstovian *Oreolagus* (Anceney, *O. nevadensis*, *O. wallacei*) and small size with two of the three. In these respects morphology of *O. colteri* seems to be somewhat intermediate between that of previously described Hemingfordian and Barstovian species.

Family Leporidae Gray, 1821

Subfamily Archaeolaginae Dice, 1929

Genus *Hypolagus* Dice, 1917

Hypolagus, species indeterminate

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Hemingfordian to late Blancan of western North America, mid-Pliocene(?) of Asia, Villafranchian of Asia and Europe (Dawson, 1958).

Referred specimens.—Lower M, KUPV 17818. P², UWBM 62696. Upper M, UWBM 62699, 62700, 62706, 62710, 62713, KUPV 17816, 17817, 65679. KUPV specimens from UWBM loc. C0236, others from loc. C0237.

Measurements.—Table 3.

Table 3.—*Dental measurements, Hypolagus and Archaeolagus emeraldensis, new species, Colter Formation.*

Tooth	Specimen	AP	TA	TP	T
<i>Archaeolagus emeraldensis</i>					
P ₃	AMNH 89726	2.8	—	2.1	—
P ₄	AMNH 89801	2.7	2.7	2.6	—
M ₁	AMNH 89801	2.9	2.9	2.7	—
M ₂	AMNH 89801	3.0	2.7	2.6	—
<i>Hypolagus</i> , species indeterminate					
P ²	UWBM 62696	1.1	—	—	1.9
M*	UWBM 62699	1.4	—	—	2.5
M*	UWBM 62700	1.5	—	—	2.6
M*	UWBM 62713	1.4	—	—	2.5

* Molariform upper tooth.

Discussion.—Because most of the teeth are broken and worn, and P₃ is not represented, species determination was not possible. The well developed reentrant and shallow external groove on the anterior surface of P², combined with slightly crenulated hypostria on some molariform teeth, identify the genus as *Hypolagus*.

Archaeolagus emeraldensis, new species

Plate III I, K

Holotype.—AMNH 89726, P₃.

Hypodigm.—AMNH 89801, mandible with P₄–M₂.

Type locality.—Emerald Lake SR, UWBM loc. C0241.

Etymology.—For type locality.

Age.—Late Arikareean.

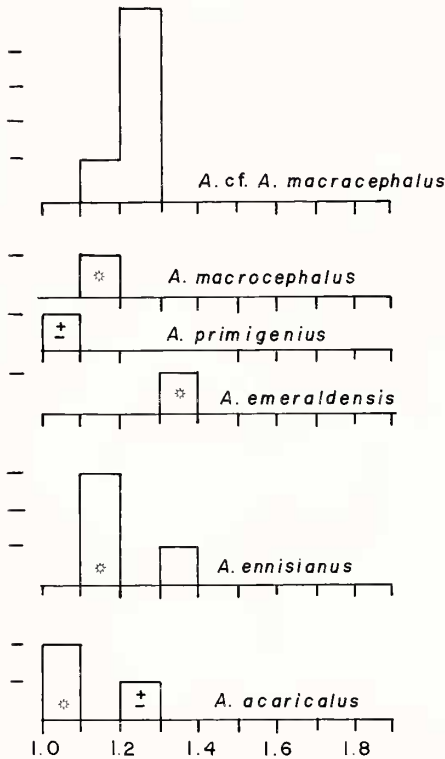
Range of other named species of genus. Arikareean: John Day Formation of northeast Oregon (*A. ennisianus* Cope, 1881) (Dawson, 1958). Tick Canyon fauna of southern California (*A. acaricolus* Dawson, 1958) (Whistler, 1967). Late Arikareean: Standing Rock local fauna northwest of Albuquerque, New Mexico (*A. cf. A. macrocephalus*) (Gawne, 1976). Hemingfordian: Rosebud Formation of Wounded Knee area, South Dakota (*A. macrocephalus* Matthew, 1907; *A. primigenius* Matthew, 1907) (Dawson, 1958; MacDonald, 1963).

Referred specimens.—Holotype and paratype only known specimens.

Diagnosis.—Larger than *A. acaricolus* and *A. ennisianus*, smaller than average *A. macrocephalus* (see Fig. 11 and Table 3). P₃ more elongate than in *A. primigenius*, *A. macrocephalus*, and *A. acaricolus*, with ratio AP/T near 1.33, anteroexternal groove facing more labiad than in *A. primigenius*. P₄–M₂ talonids wide, with ratio of trigonid width/talonid width commonly between 1.0 and 1.1.

Description and comparison.—Lower cheek teeth

P₃ RATIO AP/T
IN *ARCHAEOLAGUS*



LENGTH OF LOWER
TEETH IN *ARCHAEOLAGUS*

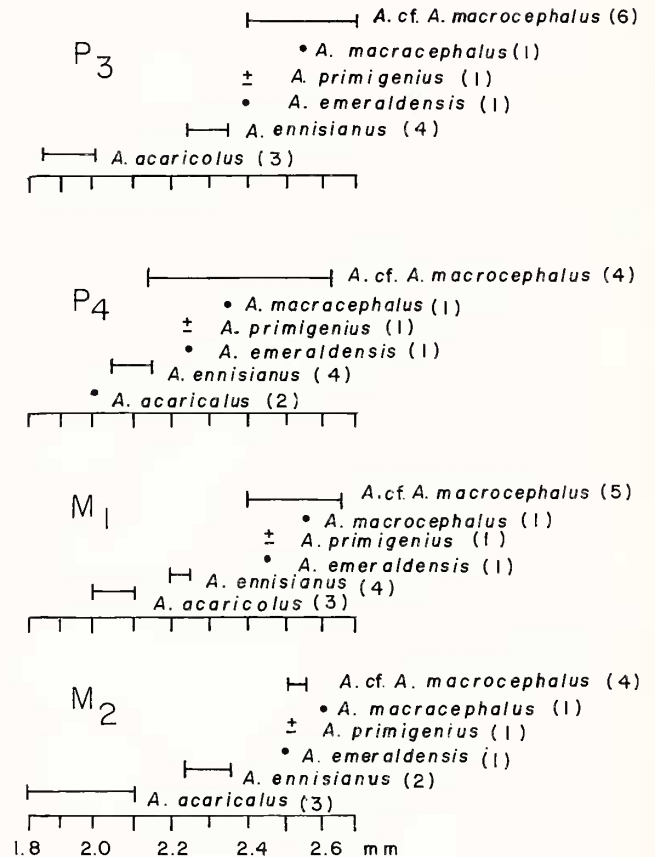


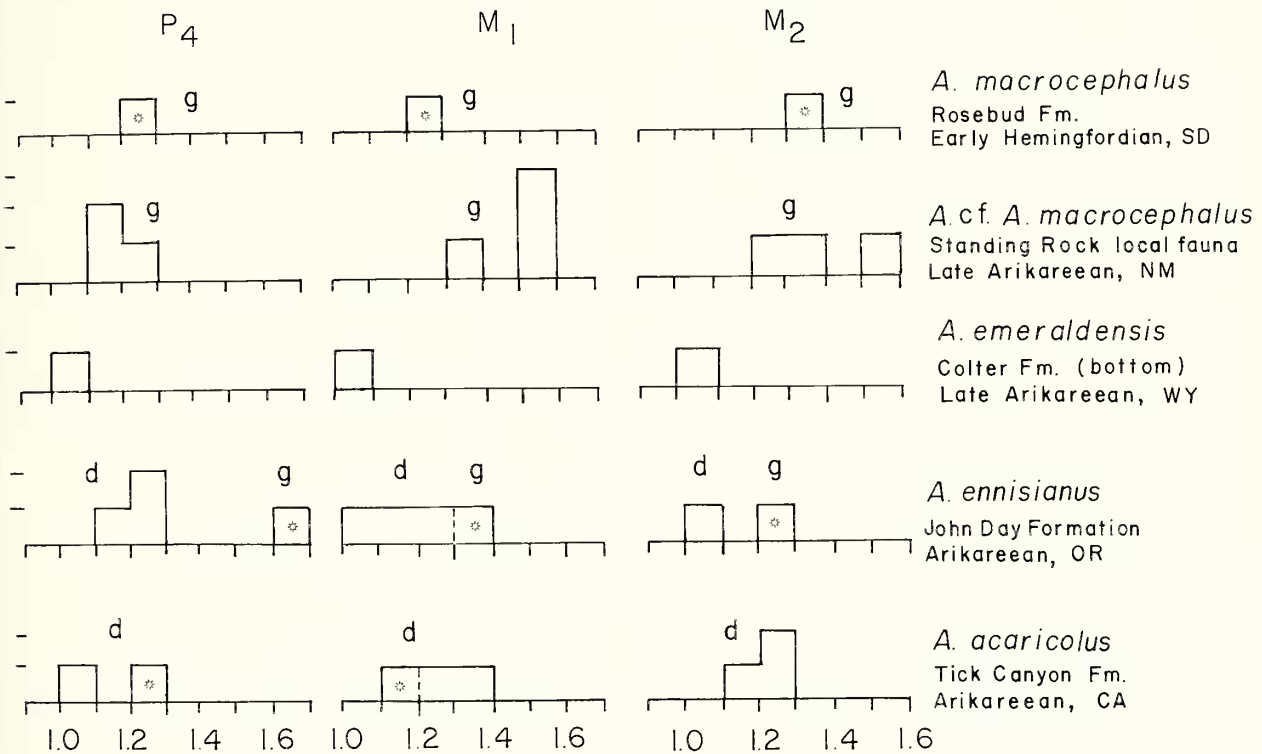
Fig. 11.—Left: Comparisons of the ratio AP/T in species of *Archaeolagus*. Right: Comparisons of the length of lower cheekteeth in species of *Archaeolagus*. Bars illustrate the observed range; the number of measured specimens is shown in parentheses. Data for *A. cf. A. macrocephalus*, *A. macrocephalus*, and the type of *A. ennisianus* from Gawne (1976); for others except *A. emeraldensis* from Dawson (1958). A star indicates a type specimen.

of *A. emeraldensis* (Pl. III I, K) are larger than those of *A. acaricolus* and *A. ennisianus* but somewhat smaller than usual for *A. macrocephalus* and *A. cf. A. macrocephalus* (Fig. 11). As in *A. ennisianus*, the P₃ is long (Fig. 11) with a shallow anteroexternal groove that faces mainly labiad. The portion anterior to this groove is shorter in three specimens of *A. cf. A. macrocephalus* figured by Gawne (1976), and P₃ as a whole is relatively shorter in these and in the type of *A. macrocephalus* (Fig. 11). Even shorter P₃'s, with the anteroexternal groove facing more anterad, characterize *A. primigenius* and *A. acaricolus* (Dawson, 1958). The posteroexternal reentrant, which is the only external groove filled with cement, extends about halfway across the tooth in *A. emeraldensis*. The P₃ differs from those of Paleolaginae in possessing more than one external

groove, and from *Hypolagus* in lacking a relatively deep and cement-filled anteroexternal groove.

P₄–M₂ (Pl. III I) of *A. emeraldensis* show the general leporid pattern, but relatively wide talonids make them distinct from most other species (Fig. 12). A P₄ of *A. acaricolus* (LACM CIT 5172) and an M₂ of *A. ennisianus* (YPM unnumbered, Dawson, 1958) resemble the Emerald Lake specimen. On M₂, the lingual margin of the talonid is nearly twice as long as the labial margin.

Discussion.—In its larger size *A. emeraldensis* may be slightly more advanced than *A. ennisianus*, but the long P₃ and wide talonids suggest a relatively close relationship between the two. Because *A. macrocephalus* and *A. cf. A. macrocephalus* both share even larger size and narrow talonids, these species seem to be farther removed. *Archaeolagus acari-*

RATIO TA/TP IN LOWER TEETH OF *ARCHAEOLAGUS*

Sources for comparative measurements: d=Dawson (1958), g=Gawne, (1976). *Type specimen.

Fig. 12.—Comparison of the ratios TA/TP for lower teeth in species of *Archaeolagus*.

colus shows least similarity to *A. emeraldensis*, judging from the short P_3 and small size. *A. primigenius*, by virtue of the short P_3 , appears more closely related to *A. acaricolus* than to *A. emeraldensis*.

AMNH 89801 and the type of *A. emeraldensis* may represent the same individual, because the teeth are similarly worn and the P_3 fits well into the portion of the alveolus that remains in AMNH 89801. The paucity of fossils at the very small exposure increases the likelihood that only one individual is represented.

Order Rodentia Bowditch, 1821
 Family Scuridae Gray, 1821
 Subfamily Sciurinae Baird, 1857
 Genus *Spermophilus* Cuvier, 1825

Spermophilus (Otospermophilus), near
S. (O.) primitivus Bryant, 1945
 Plate II J–L

Locality.—North Pilgrim 2, UWBM loc. C0237.

Age.—Late Barstovian.

Range of morphologically similar species.—Fig. 13.

Referred specimens.— M_1 or M_2 , UWBM 62733, 62739. M_3 , UWBM 62742, 62736, 62741. M^1 or M^2 , UWBM 62737, 62740, 62746.

Measurements.—Table 4 and Black (1963), Storer (1975), Lindsay (1972), and Barnosky (1983).

Description and comparison.—The molars from Jackson Hole are larger than those of *Tamias* and *Miosciurus*, but smaller than in *Protosciurus*, *Palearctomys*, *Arctomyoides*, *Paenemarmota*, *Marmota*, *Protospermophilus*, and most species of *Spermophilus* (Black, 1963). *Amnospermophilus* differs in having an M_3 commonly wider than long, and on M^{1-2} a constriction separating the metaloph from the protocone. Species with molars similar in size to the Jackson Hole material include *Spermophilus primitivus*, which is only slightly larger (lower molars 2.1–2.7 mm AP, Black, 1963), *S. tephurus* (Black, 1963), *S. sp.* from Kleinfelder Farm (Storer, 1975), *Miospermophilus bryanti* (Black, 1963), and *M. sp.* from Barstow (Lindsay, 1972). *S. tephurus* differs in possessing a large mesostyle located next to the

		RANGE OF <i>SPERMOPHILUS</i> AND <i>MIOSPERMOPHILUS</i>										• TYPE LOCALITY
FAUNA FM LOCATION	BARSTOW " SAN BERNADINO CO., CA	SKULL SPG. (RED BASIN) MALHEUR CO., OR	RED BASIN BUTTE CR. VS. MALHEUR CO., OR	ANCENEY MADISON V. GALLATIN CO., MT	FLINTCREEK GRANITE CO., MT	QUARRY A ARIKAREE LOGAN CO., CO	SPLIT ROCK FREMONT CO., WY	SNAKE CREEK " " SIOUX CO., NB. S. SASKATCH.	KLEINF. FM. WOOD MT S. SASKATCH.	CUNNINGHAM COLTER TETON CO., WY		
HEMP-HILLIAN											<i>S. matthewi</i> • Black, 1961 Skinner, 1977	
CLARENDONIAN	LATE											
	EARLY											
BARSTOVIAN	LATE	<i>M. sp.</i> Lindsay, 1972	according to Shotwell, 1968 ↑ ?	<i>S. tephrus</i> Shotwell, 1968	<i>S. sp.</i> Sutton, 1977	<i>S. primitivus</i> • Black, 1961, 1963					<i>S. sp.</i> Storer, 1975	<i>S. near S. primitivus</i>
	EARLY	<i>M. sp.</i> Lindsay, 1972										
HEMING-FORDIAN		<i>S. tephrus</i> • Black, 1963				<i>M. bryanti</i> • Wilson, 1960 Black, 1963	<i>M. wyomingensis</i> Black, 1963 • Munthe, 1979a					

Fig. 13.—Geographic and stratigraphic range of some Miocene species of *Spermophilus* and *Miospermophilus*.

metacone and a narrow anterior cingulum. In contrast, the Jackson Hole species has a small, centrally located mesostyle and an expanded anterior cingulum. The posterolingual corners of M_1 and M_2 show more reduction and rounding in *S. sp.* than in the teeth from Jackson Hole, judging from descriptions and illustrations by Storer (1975:74). *Miospermophilus wyomingensis* has sharp crests on lophs and cusps of upper molars, incomplete metalophids on M_1 – M_2 , and absence of metalophid on M_3 . Fossils from Jackson Hole differ in having low rounded cusps and lophs, complete metalophid that isolates a small trigonid on M_1 , and an incomplete but prominent metalophid on M_3 . Unlike *M. sp.* from Barstow, an obvious parastyle occurs on M_1 – M_2 of the Jackson Hole species, as does a mesostylid on M_1 – M_2 . The Jackson Hole species shares some characters with *M. bryanti*, but more with *S. primitivus*, and is therefore referred to *Spermophilus* (Table 5). Available material from Jackson Hole differs from *S. primitivus* in its distinctly smaller size and small rather than large mesostyle, and it may therefore represent a new species. The *Spermophilus* from

Anceney, reported in an unpublished doctoral dissertation by Sutton (1977), resembles the Jackson Hole material except for slightly larger size.

Discussion.—Small size, moderately well developed metalophids, and only slight curvature of the entoconid area in the Jackson Hole specimens resemble conditions in primitive species of *Spermophilus*. The two species that bear closest resemblance, *S. primitivus* of the Flint Creek fauna and *S. sp.* from Anceney, are both from Rocky Mountain deposits of late Barstovian age.

Tamias Illinger, 1811

Tamias cf. *T. ateles* (Hall), 1930

Miospermophilus Sutton and Black, 1972.

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of species.—Late Barstovian: Barstow fauna of San Bernardino County, California (Lindsay, 1972). Tonapah fauna of Nye County, Nevada (Black, 1963; Henshaw, 1942). Early Clarendonian: Matthews Ranch fauna of the Cuyama Badlands, Cal-

Table 4.—*Dental measurements, Spermophilus near S. primitivus, Colter Formation, North Pilgrim 2.*

Tooth	Specimen	AP	T	AP/T
M ¹ or ²	UWBM 62740	1.7	2.2	0.77
M ¹ or ²	UWBM 62746	1.8	2.2	0.87
M ¹ or ²	UWBM 62737	1.6	—	—
M ₁ or ₂	UWBM 62739	1.5	1.9	0.79
M ₁ or ₂	UWBM 62733	—	2.1	—
M ₃	UWBM 62741	2.0	1.8	1.11

ifornia (James, 1963). Late Clarendonian: Nettle Springs fauna of the Cuyama Badlands, California (James, 1963).

Referred specimens.—P₄, UWBM 62735. M₁ or M₂, UWBM 62734, 62735. M₃, UWBM 62738. M¹ or M², UWBM 62833, 62834, 62836. UWBM 62734, 62735, and 62738 from UWBM loc. C0237, others from loc. C0236.

Measurements.—Table 6.

Description and comparison.—These teeth are referred to *Tamias* on the basis of small size, very low and somewhat bulbous crowns, and marked anterior bowing of the anterior cingulid. *Miosciurus* differs in the less bowed anterior cingulid and more rounded posterolingual corner on lower molars (see Black, 1963:pl. 2, fig. 3). In *Ammospermophilus* of the Miocene, the protocone and metaloph tend to connect, especially in P⁴ and M¹, the mesostyle is usually more prominent, and molars are usually slightly larger than in *Tamias* and teeth from Jackson Hole (James, 1963; Lindsay, 1972).

Upper molars from the Jackson Hole closely resemble those of *T. ateles*, which have been described in detail by Black (1963) and Lindsay (1972). In the only complete and unworn specimen of M¹ or M², the mesostyle is slightly smaller and the anterior cingulum is less expanded than in the type specimen. In view of these minor differences, referral to *T.*

Table 6.—*Dental measurements, Tamias cf. T. ateles, Colter Formation.*

Tooth	Specimen	AP	T	Locality
M ¹ or ²	UWBM 62836	1.3	1.6	Cunningham Hill
M ¹ or ²	UWBM 62834	1.4	1.7	Cunningham Hill
P ₄	UWBM 62735	1.4	1.3	North Pilgrim 2
M ₁ or ₂	UWBM 62835	1.4	1.7	Cunningham Hill
M ₁ or ₂	KUVP 17487	1.4	1.7	Cunningham Hill
M ₁ or ₂	UWBM 62734	1.3	1.5	North Pilgrim 2
M ₃	UWBM 62738	—	1.4	North Pilgrim 2

ateles is tentative. Lower molars are nearly identical to *T. ateles* from Tonapah figured by Black (1963: pl. 2, fig. 2).

Tamias sp. from the Arikarean Sharps Formation (Black, 1963), Hemingfordian Thomas Farm fauna of Florida, and Hemingfordian Martin Canyon Quarry A fauna show stronger union of the metaloph and protocone. In *T. ateles*, *T.* sp. from Kleinfelder Farm (Storer, 1975:fig. 53g), and *Tamias* of the Colter Formation, the two structures do not meet. A less reduced posterolingual portion of the M₁–M₂ differentiates the Kleinfelder form and the Split Rock *T.* sp. from the Colter material.

Subfamily Petauristinae Simpson, 1945

Genus *Petauristodon* Engesser, 1979

Petauristodon, species indeterminate

Plate II M

Locality.—North Pilgrim 2, UWBM loc. C0237.

Age.—Late Barstovian.

Range of genus.—Fig. 14.

Referred specimen.—M₃, UWBM 62743.

Measurements.—AP = 3.2 mm. T = 3.3 mm.

Table 5.—*Comparison of Spermophilus from Colter Formation, Miospermophilus bryanti, and Spermophilus primitivus.*

1. Characters shared by all three species <ol style="list-style-type: none"> Size (<i>S. primitivus</i> slightly larger) High parastyles Wide anterior cingulum Metaloph joins protocone obliquely Corner of entoconid slightly curved 	2. Condition in <i>M. bryanti</i> <ol style="list-style-type: none"> Posterolophid high Mesostylid small, mesoconid absent
2. Characters shared by Jackson Hole species and <i>S. primitivus</i> <ol style="list-style-type: none"> Posterolophid low Distinct mesostylid and mesoconid although slightly less in Jackson Hole species Metalophid weak, isolates small trigonid basin on M₁ but not on M₂ 	c. Trigonid basin isolated on both M ₁ and M ₂
3. Characters shared by Jackson Hole species and <i>M. bryanti</i> <ol style="list-style-type: none"> Mesostyle small 	3. Condition in <i>S. primitivus</i> <ol style="list-style-type: none"> Mesostyle large

		RANGE OF <i>PETAURISTODON</i>						● TYPE LOCALITY
FAUNA FM	LOCATION	BARSTOW SAN BERNADINO CO., CA	DOME SPRING CALIENTE	MATTHEWS RCH. CALIENTE	NETTLE SPRING CALIENTE	RED BASIN BUTTE CR. VS. MALHEUR CO., OR	KLEINF. FM. WOOD MT.	CUNNINGHAM COLTER TETON CO., WY
HEMP-HILLIAN								
CLARENDONIAN	LATE				<i>P. matthewsi</i> ● James, 1963			
	EARLY			<i>P. matthewsi</i> <i>P. sp.</i> James, 1963				
BARSTOVIAN	LATE	<i>P. jamesi</i> ● <i>P. minimus</i> ● Lindsay, 1972	<i>P. uphami</i> ● James, 1963			<i>P. sp.</i> Shotwell, 1968	<i>P. sp.</i> Storer, 1975	<i>P. sp.</i>

Fig. 14.—Geographic and stratigraphic range of *Petauristodon*.

Description and comparison.—Lophids in the central basin of UWBM 62743 (Pl. II M) are better defined than in the only other complete M₃ that has been described, that of *P. matthewsi*. The Jackson Hole species further differs from *P. matthewsi*, as well as from *P. sp.* of Kleinfelder Farm, in having a larger M₃. The M₃ of *P. jamesi*, from which the anterior third is broken, has a less expanded posterointernal margin than the Jackson Hole specimen. Although M₃ is unknown for *P. sp.* of Red Basin, it was probably larger than UWBM 62743; the P₄'s from Red Basin range from 3.48 to 4.23 mm in width. The Jackson Hole form cannot be differentiated from *P. sp.* of Matthews Ranch, in which morphology of the worn M₁–M₂ falls within the range to be expected in the dentition represented by UWBM 62743. *P. uphami* is known only by upper teeth.

Sciuridae, species indeterminate

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Referred specimens.—Molar fragments, KUVF 65678 from UWBM loc. C0236, UWBM 62747 from loc. C0237.

Discussion.—Both specimens are much larger than molars of *Spermophilus primitivus*, but too worn and broken for even generic assignment.

Family Aplodontidae Troussart, 1897
Subfamily Allomyinae Marsh, 1877
Genus *Allomys* Marsh, 1877
Allomys cristabrevis, new species
Plate II C

Holotype.—AMNH 89727, M₁.

Type locality.—Emerald Lake SR, UWBM loc. C0241.

Etymology.—Crista (crest) and brevis (short) referring to the diagnostically short, blunt crests.

Age.—Late-early Arikareean.

Range of most closely related species.—Late-early Arikareean (*Meniscomys* Concurrent-range Zone): fauna of Monroe Creek Formation from Wounded Knee area, South Dakota (*Allomys harkseni* MacDonald, 1963) (J. R. MacDonald, 1970; L. J. MacDonald, 1972). John Day Formation, central Oregon (*Allomys cavatus* Cope, 1881) (Rensberger, 1983).

Referred specimens.—Type only known material.

Diagnosis.—M₁ (only known tooth) large (2.7 mm AP), metaconid positioned near center of anterior border, internal crests more blunt than in any other species, extending less far toward center of tooth than in other species except *A. cavatus*, posterolabial fossettid not fully formed.

Description and comparison.—As in all M₁'s of *Allomys* the crests in AMNH 89727 are more prominent than in *Parallomys* Rensberger, 1983, but low-

RANGE OF MONOSAULAX

FAUNA FM LOCATION	• TYPE LOCALITY															
	BARSTOW SAN BERNADINO CO., CA	N. COALINGA SAN JOAQUIN VALLEY, CA	OUARTZ B. DEER BUTTE MALHEUR CO., OR	RED BASIN BUTTE CR. VS. MALHEUR CO., OR	VIRGIN VALLEY HUMBOLDT CO., NV	LOW CEDER MT. MINERAL CO., NV	ANCENEY MADISON V. GALLATIN CO., MT	GALLATIN CO., MT	'SANTA FE' NEW MEXICO	EUBANKS OGALLALA NE CO.	OUARRY A. ARIKAREE LOGAN CO., CO	L. SNAKE CRK. OLCOTT ? NEBRASKA	NIORBARA R. VALENTINE CHERRY CONE	BATESLAND BENNETT CO., SD	KLEINF. FM WOOD MT. S. SASKATCH.	CUNNINGHAM COLTER TETON CO., WY
HEMPHILLIAN																
CLARENDONIAN	LATE															
	EARLY						<i>M. pansus</i> Stirton, 1935		<i>M. pansus</i> Stirton, 1935							
BARSTOVIAN	LATE	<i>M. pansus</i> Lindsay, 1972	<i>M. pansus</i> ?	<i>M. progressus</i> Shotwell, 1968	<i>M. typicus</i> • Shotwell, 1968		<i>M. near M. curtus</i> Sulton, 1977 Darr, 1956	<i>M. complexus</i> Stirton, 1935	<i>M. pansus</i> Stirton, 1935				<i>M. pansus</i> Stirton, 1935	<i>M. curtus</i> • Stirton, 1935	<i>M. cf. M. pansus</i> Storer, 1975	<i>M. cf. M. curtus</i>
	EARLY		<i>M. pansus</i> Bode, 1935			<i>M. pansus</i> ? Stirton, 1935				<i>M. curtus</i> Galbreath, 1953		<i>M. pansus</i> Stirton, 1935	<i>M. curtus</i>			
HEMINGFORDIAN													<i>M. sp</i> Wilson, 1960		<i>M. sp</i> Martin, 1976	

Fig. 15.—Geographic and stratigraphic range of *Monosaulax*.

er than in *Alwoodia magna* Rensberger, 1983. Unlike *Alwoodia magna* and most *Allomys*, however, the internal crests are more blunt in *A. cristabrevis*, much like the condition in *A. cavatus*.

In contrast to *Allomys cavatus*, *A. simplicidens* Rensberger, 1983, *A. reticulatus* Rensberger, 1983, and *A. tessellatus* Rensberger, 1983, the M_1 of *Allomys cristabrevis* is large, measuring 2.7 mm AP \times 2.4 mm T. It further differs in location of the metaconid near the center of anterior border. In the other four species, the metaconid is positioned near the lingual margin of the tooth. The M_1 of *A. nitens*, evidenced by UCMP 107717, UWBM 58058, and UWBM 51967, somewhat resembles the Jackson Hole specimen in size and less lingual position of the metaconid. Even in these specimens, however, the metaconid is more linguallly positioned. The M_1 in *A. nitens*, *A. cavatus*, *A. simplicidens*, *A. reticulatus*, and *A. tessellatus* shows a flat lingual margin, unlike the bulging margin of the M_1 in *A. cristabrevis*. The same species differ from *A. cristabrevis* in having a crest that connects the mesoconid and hypoconulid to isolate a lake near the hypoconid. The crests are too short to isolate a lake on M_1 of *A. cristabrevis*. *Alwoodia magna* resembles the Jackson Hole specimen in the bulging lingual margin, but resembles the other species of *Allomys* in the possession of a hypoconid lake and connection of the metaconid and entoconid by a minor crest. The M_1 of one specimen of *Allomys harkseni*, SDSM 6273 (MacDonald, 1970), is very similar to the Jackson Hole specimen, differing only in the slightly longer crest emanating from the metaconid, longer

posterior arm of the protoconid, and slightly more elongate mesoconid that isolates a hypoconid lake after considerable wear. Four other M_1 's (LACM 120347, 120348, 120352, 120353, reported as LACM 23525, 23526 in MacDonald, 1972) of *A. harkseni* additionally differ in the prominent junction of the mesoconid and hypoconid crests as well as anterior extension of the hypoconulid. Because of these longer crests, 3 lakes occur when the posterior half of the tooth is worn, unlike the single transversely elongate lake in *A. cristabrevis*. Other M_1 's of "*A. harkseni*" reported by MacDonald (1970) and MacDonald (1972) from LACM loc. 1871 differ considerably in the thinner, more convoluted crests.

Discussion.—AMNH 89727 most closely resembles two species that occur in the *Meniscomys* Concurrent-range zone. Except for slight advancement in central extension of crests, referred teeth of *Allomys harkseni* from the upper part of the zone (Monroe Creek Formation) are virtually identical to the M_1 of *Allomys cristabrevis*. The species are particularly similar in the labial position of the metaconid, bulging lingual margin, blunt crests, and large size. The Jackson Hole species is probably slightly older, perhaps equating with the middle of the *Meniscomys* Concurrent-range Zone, because the blunt shorter crests are a primitive feature that indicate an earlier stage in heightening and extending internal crests toward the middle of the tooth. Rensberger (1982, 1983), in thoroughly documenting evolutionary sequences in allomyines, cited blunt short crests as a primitive character. In the John Day Formation, only *Allomys cavatus* has crests as blunt

and short as *A. cristabrevis*, but is slightly more advanced in closure of the hypoconid lake and somewhat flatter lingual margin. The type locality for *A. cavatus* is not known, but probably occurs below the middle of the *Meniscomys* Concurrent-range Zone (Rensberger, 1983). *Alwoodia magna*, the only North American allomyine with which *Allomys cristabrevis* and *Allomys harkseni* share the primitive feature of a lingually convex M_1 , is restricted to the lower part of the *Meniscomys* Concurrent-range Zone in the John Day Formation.

Subfamily Meniscomyinae Rensberger, 1981

Genus *Niglarodon* Black, 1961

Niglarodon sp.

Locality.—Emerald Lake SR, UWBM loc. C0241.

Age.—Late Arikareean.

Range of most closely related species.—Late-early Arikareean: Upper *Meniscomys* Concurrent-range Zone, Deep River Formation, Meagher County, Montana (*N. blacki* Rensberger, 1981).

Referred specimens.—AMNH 89725, mandible with P_4 – M_3 , AMNH 89800, maxilla with P^4 – M^3 .

Discussion.—These specimens will be described by M. C. McKenna, who generously provided casts for my inspection. Rensberger (1981), on the basis of the illustrated jaw (Love et al., 1976), referred the form to *Niglarodon* and noted a possible affinity to *N. blacki*.

Family Castoridae Gray, 1821

Genus *Monosaulax* Stirton, 1935

Monosaulax, cf. *M. curtus* (Matthew and Cook), 1909

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of similar species.—Figure 15.

Referred specimens.— P_4 , KUVF 17484. P^4 , KUVF 17483.

Measurements.— P_4 , AP = 3.8 mm, T = 3.0 mm on occlusal surface, AP = 4.0 mm, T = 3.1 mm at base of crown. P^4 , AP = 3.0 mm, T = 3.0 mm on occlusal surface, AP = 3.3 mm, T = 3.3 mm at base of crown.

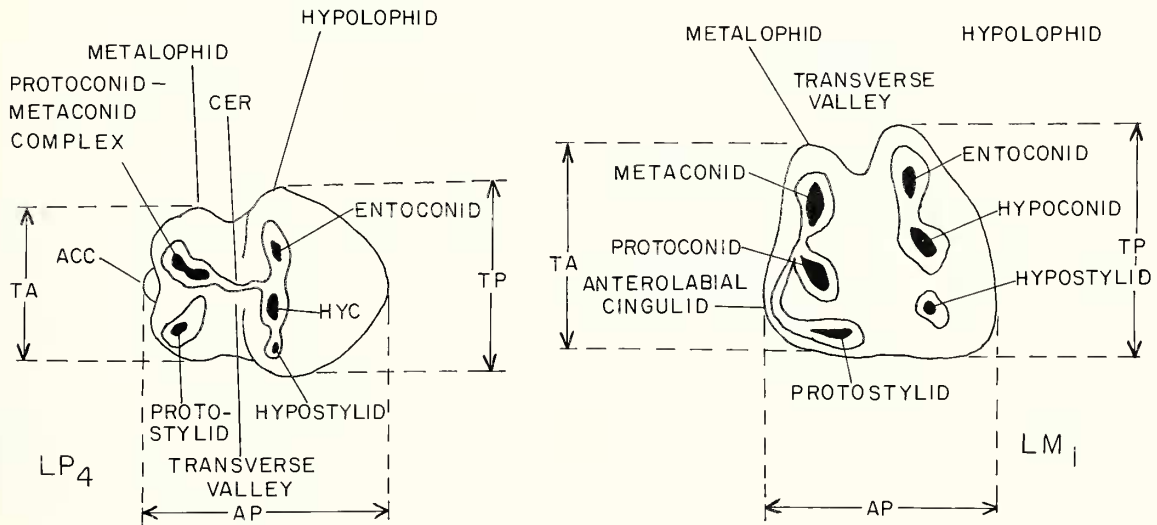
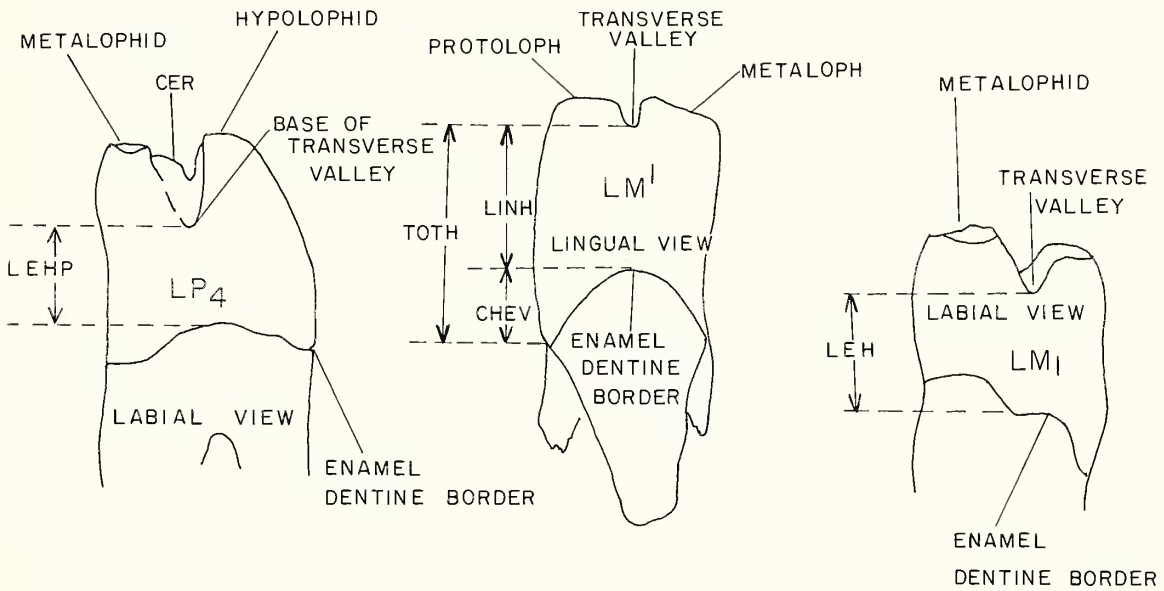
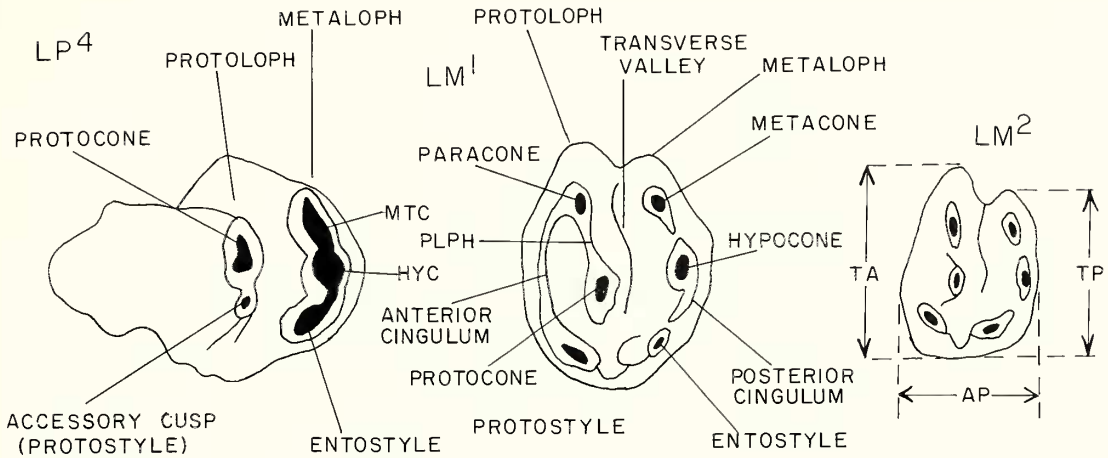
Description and comparison.—In occlusal pattern, the premolars resemble similarly worn specimens of *Monosaulax pansus* (UCMP 31449) and *M. curtus* (type, AMNH 13871) illustrated by Stirton (1935). The teeth from Jackson Hole, which are too small for assignment to pre-Barstovian species or *M. pansus*, approximate those of *M. curtus*, *M. near curtus*, *M. complexus*, *M. typicus*, and *M. progressus* in size. Premolars are not known for *M. complexus*, *M. typicus* and *M. progressus* (Shotwell, 1968) differ in possessing a hypoflexus and para-flexus that overlap near the midline of P^4 in occlusal view. These two structures touch but do not overlap in *M. near curtus* from Ancney (Sutton, 1977; Dorr, 1956) and the Jackson Hole material. *M. progressus* further differs in the prominent anterior stylid on P_4 and anterolingual groove on P^4 , both of which are absent in the premolars from Jackson Hole.

Discussion.—The teeth from Jackson Hole provide the third record of *Monosaulax* from the northern Rocky Mountains. The presence of different wear stages and different teeth complicate comparison to fossils from Ancney (*M. near curtus*) and Gallatin County, Montana (*M. complexus*), but beavers from all three localities are smaller than is normal for *M. pansus*. The material from Jackson Hole cannot be differentiated from the Great Plains species *M. curtus*, but because only 2 worn specimens comprise the sample referral is tentative. Stout, on the basis of his unpublished studies, believed "*Monosaulax curtus*" to be the junior synonym of "*Eucastor curtus*," specimens of which he tentatively identified from the Fort Randall Formation of Nebraska (in Skinner and Taylor, 1967:47–49). Here I follow the majority opinion in considering *Monosaulax* a valid name, while recognizing that the relationship between *Monosaulax* and *Eucastor* deserves more detailed study.

Superfamily Geomyoidea Weber, 1904

Teeth of geomyoid rodents form the Colter Formation share the basic pattern shown in Fig. 16. Criteria listed in Fig. 17 serve to separate the genera.

Fig. 16.—Dental morphology, terminology, and definition of measurements in geomyoids. Abbreviations—MTC, metacone. HYC, hypocone. PLPH, protolophule. TA, greatest transverse width across anterior half of tooth. TP, greatest transverse width across posterior half of tooth. T, = TA or TP, whichever is greater. AP, longest anteroposterior dimension of tooth (transverse measurements are taken perpendicular to AP). CER, central enamel ridge (in some taxa, a central enamel pit occurs in place of the CER). TOTH, total crown height. LINH, lingual crown height. CHEV, height of enamel chevron. LEH, labial enamel height of lower molar. LEHP, Labial enamel height of lower premolar.



DISTINGUISHING FEATURES BETWEEN GENERA OF GEOMYOIDS FROM THE COLTER FORMATION

CHARACTER	SIZE						
	Large 1.7 to 2.1 mm <i>Lignimus</i> <i>Mojavemys</i>	Medium 1.4 to 1.7 mm <i>Diprionomys</i> <i>Peridiomys</i>	Small 0.8 to 1.5 mm <i>Proheteromys</i> , <i>Perognathus</i> , <i>Cupidinimus</i>				
Width (T) of M ¹⁻² / ₁₋₂							
	OCCLUSAL PATTERN						
Molar Lophids	<i>Lignimus</i> (1) V-SHAPED JOIN CENTRAL	<i>Mojavemys</i> (2) STRAIGHT JOIN LABIAL	<i>Diprionomys</i> (3) = 2	<i>Peridiomys</i> (4) = 2	<i>Proheteromys</i> (5)	<i>Perognathus</i> (6) = 2	<i>Cupidinimus</i> (7) = 2
P ₄ Protoloph	JOIN METALOPH CENTRAL	JOIN METALOPH LINGUAL	= 2		= 2	= 1	= 1
P ₄	CENTRAL PIT FORMS WITH WEAR	LOPHIDS JOIN CENTRAL	LOPHIDS JOIN FIRST LABIAL CENTRAL PIT FORMS				= 2
Enamel Thickness	THICK	= 1	THICK EXCEPT POSTERIOR PART OF M ¹⁻²	THIN	= 4	= 4	= 4
	HYPSONDONTY						
Lower Molars LEH	LOW CROWN 0.6 to 0.7 mm	MEDIUM-HIGH 0.6 to 1.0 mm	HIGH 0.7 mm	LOW 0.5 to 0.6 mm	LOW	LOW 0.5 mm	MEDIUM 0.6 to 0.8 mm
Upper Molars LINH		1.0 to 1.1 mm unworn LINH/T = 0.59 to 0.65	0.8 to 1.0 mm worn	0.8 mm unworn LINH/T = 0.50			0.6 to 0.8 mm unworn LINH/T = 0.46 to 0.62
Upper Molar Roots		LABIAL FUSION 0.5 to 0.6 mm ABOVE CROWN	LABIAL FUSION 0.6 to 0.7 mm	LABIAL FUSION 0.2 mm			LABIAL FUSION 0.3 to 0.5 mm
Basal Bulge of Crown Wall	SLIGHT	= 1	STRAIGHT	STRAIGHT TO VERY SLIGHT	OBVIOUS	= 5	= 3

Fig. 17.—Morphologic characters that differentiate genera of geomyoid rodents that occur in the Colter Formation. The symbols =1, =2, =3, etc. indicate that the character is the same as in taxon (1) *Lignimus*, (2) *Mojavemys*, (3) *Diprionomys*, etc.

Family Heteromyidae Allen and Chapman, 1893
Subfamily Perognathinae Coues, 1875
Genus *Perognathus* Wied-Neuwied, 1839

Perognathus furlongi Gazin, 1930

Localities.—North Pilgrim 2, UWBM loc. C0237.
Cunningham Hill, UWBM loc. C0236.
Age.—Late Barstovian.

Range of middle Miocene species.—Fig. 18.

Referred specimens.—M₁, KUVF 17810, UWBM 62612, 62697.
P₄, KUVF 17808, 17801, UWBM 62789. UWBM 62612 from UWBM loc. C0237, others from UWBM loc. C0236.

Measurements.—Table 7 and Korth (1979), Lindsay (1972), James (1963), Gazin (1930), Barnosky (1983).

Description and comparison.—The brachyodont cheek teeth from Jackson Hole show the typical pattern for *Perognathus* (Fig. 16), which has been described in detail by Wood (1935), James (1963), and Lindsay (1972) among others. Crowns have bulbous bases, and the loph(ids) of the premolars join centrally. Of known Barstovian and Clarendonian species, teeth of *P. minutus* and *P. trojectioansrum* are smaller than those from Jackson Hole. Material from Jackson Hole falls within the known size range for *P. furlongi* and the Anceney *P. sp. A* (Sutton,

RANGE OF *PEROGNATHUS*

● TYPE LOCALITY

FAUNA FM	BARSTOW	DOME SPRING	MATTHEWS R.	NETTLE SPRING	ANCENEY	ANNIES GCO	CUNNINGHAM
LOCATION	SAN BERNADINO CO, CA	CALIENTE	CALIENTE	CALIENTE	MADISON V. GALLATIN CO, MT	VALENTINE	COLTER
	CUYAMA VALLEY, CA				KNOX CO., NB		TETON CO, WY
HEMPHILLIAN							
CLARENDONIAN	LATE			<i>P. furlongi</i> ● Gazin, 1930 James, 1963			
	EARLY		<i>P. furlongi</i> <i>P. minutus</i> ● James, 1963				
BARSTOVIAN	LATE	<i>P. furlongi</i> <i>P. minutus</i> Lindsay, 1972	<i>P. furlongi</i> James, 1963		<i>P. sp. A</i> <i>P. sp. B</i> Sutton, 1977	<i>P. furlongi</i> <i>P. trojectionansrum</i> ● Korth, 1979	<i>P. furlongi</i>
	EARLY	<i>P. furlongi</i> <i>P. minutus</i> Lindsay, 1972					
HEMINGFORDIAN							

Fig. 18.—Geographic and stratigraphic range of Barstovian and Clarendonian species of *Perognathus*.

1977). As commonly happens in *P. furlongi*, stylids of M₁ join with wear in the Jackson Hole material. Lower molars from Anceney more commonly show central union of the lophids (Sutton, 1977:71).

Subfamily Dipodomysinae Coues, 1875
Genus *Cupidinimus* Wood, 1935

Cupidinimus sp.
Plate IV A–L

Proheteromys Sutton and Black (1972), in part.

Localities.—North Pilgrim 2, UWBM loc. C0237, Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Early Barstovian: Barstow Formation, San Bernardino County, California (*C. halli* Wood, 1936; *C. "nebraskensis"*) (Lindsay, 1972). Late Barstovian: Barstow Formation (*C. halli* Wood, 1936; *C. halli* Lindsay, 1972). Madison Valley Formation, Gallatin County, Montana (*C. madisonensis* Dorr, 1956). Valentine Formation, Cherry, Brown, and Knox Counties, Nebraska (*C. nebraskensis* Wood, 1935) (Klingener, 1968; Korth, 1979). Wood Mountain Formation, Saskatchewan (*C. kleinfelderi* Storer, 1975; *C. saskatchewanensis* Storer, 1975). Early Clarendonian: Esmeralda Formation, Esmeralda County,

Nevada (*C. tertius* Wood, 1935; *C. quartus* Wood, 1935). Avawatz Formation, San Bernardino County, California (*C. "cf. C. tertius"*) (Wilson, 1939). Late Clarendonian: Caliente Formation, Ventura County, California (*C. cuyamensis* Wood, 1937) (James, 1963). Hemphillian: Bidahochi Formation, Navajo County, Arizona (*C. bidahochiensis* Baskin, 1979).

Referred specimens.—From UWBM loc. C0236, P₄, UWBM 62790–62793, 62798. M₁, UWBM 62800, 62801, 62803, 62807, KUVV 17494. M₂, UWBM 62809, 62813, KUVV 17805, 17806, 17809. M₃, UWBM 62805, KUVV 17811, 17812, 17814. P₄, UWBM 62787, 62788, 62794–62796, KUVV 17500, 17802. M¹, UWBM 62799, 62806, 62810, 62812, KUVV 17804. M², UWBM 62802, 62811, KUVV 17803, 17813, 17815.

From UWBM loc. C0237, P₄, UWBM 62609. M₁, UWBM 62601, 62610. M₂, UWBM 62602, 62603. M₃, UWBM 62614.

Table 7.—Dental measurements, *Perognathus furlongi*, Colter Formation.

Tooth	Specimen	AP	T	Locality
P ⁴	UWBM 62789	1.0	1.1	Cunningham Hill
P ⁴	KUVV 17801	1.1	1.2	Cunningham Hill
P ⁴	KUVV 17808	1.0	1.1	Cunningham Hill
M ₁	UWBM 62612	1.0	1.1	North Pilgrim 2
M ₁	UWBM 62797	0.9	1.1	Cunningham Hill
M ₁	KUVV 17810	1.1	1.1	Cunningham Hill

Table 8.—Dental measurements, *Cupidinimus*, Colter Formation.

Tooth	Statistic	AP	T	TA	TP
P ₄	Mean	1.12	—	0.83	1.01
	SD	0.075	—	0.042	0.058
	OR	1.0–1.2	—	0.8–0.9	0.9–1.1
	N	6	—	6	6
M ₁	Mean	1.12	—	1.24	1.29
	SD	0.065	—	0.079	0.077
	OR	1.0–1.2	—	1.1–1.4	1.2–1.4
	N	8	—	8	8
M ₂	Mean	1.00	—	1.18	1.11
	SD	0.079	—	0.057	0.102
	OR	0.9–1.1	—	1.1–1.3	0.9–1.2
	N	5	—	5	5
M ₃	Mean	0.73	—	1.0	0.8
	SD	0.058	—	0.100	0.100
	OR	0.7–0.8	—	0.9–1.1	0.7–0.9
	N	3	—	3	3
P ⁴	Mean	1.21	1.31	—	—
	SD	0.069	0.099	—	—
	OR	1.1–1.3	1.2–1.4	—	—
	N	7	10	—	—
M ¹	Mean	0.94	1.37	—	—
	SD	0.079	0.075	—	—
	OR	0.9–1.1	1.3–1.5	—	—
	N	7	7	—	—
M ²	Mean	0.92	1.26	—	—
	SD	0.044	0.089	—	—
	OR	0.9–1.0	1.2–1.4	—	—
	N	5	5	—	—

P⁴, UWBM 62594–62597, 62608. M¹, UWBM 62598, 62599. M², UWBM 62604, 62605.

Measurements.—Table 8 and Barnosky (1983, 1986).

Discussion.—Because of the abundance and complexity of the material, taxonomy of *Cupidinimus* is treated in a separate report (Barnosky, 1986). The Jackson Hole species is more advanced than *C. nebraskensis*, *C. halli*, *C. madisonensis*, *C. eurekaensis*, and *C. saskatchewanensis* in its larger size, but is smaller than post-Barstovian forms. It resembles Barstovian species in having a narrow M₂ relative to length, contrasting with the wide M₂ of post-Barstovian species. The teeth from Jackson Hole resemble those of Barstovian species in crown height. Teeth in Clarendonian species have higher crowns (Barnosky, 1986).

Subfamily Heteromyinae Coues, 1875

Genus *Peridiomys* Matthew, 1924

Plate IV M–P

Peridiomys, species indeterminate

Proheteromys Sutton and Black (1972), in part.

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Fig. 19.

Referred specimens.—M₁ or M₂, UWBM 62676, 62664, KUVP 17496. M₃, UWBM 62683. M¹ or M², UWBM 62638, 62648. KUVP 17496 from Cunningham Hill, others from North Pilgrim 2.

Measurements.—Table 9 and Wood (1935), Shotwell (1967b), Downs (1956), Barnosky (1983).

		RANGE OF <i>PERIDIOMYS</i>									
		● TYPE LOCALITY									
FAUNA FM	LOCATION	BARSTOW SAN BERNADINO CO., CA	RED BASIN BUTTE CR VS. MALHEUR CO., OR	QUARTZ B. DEER BUTTE MALHEUR CO., OR	SKULL SPG. (≈ RED BASIN)	MASCALL " N. CENTRAL OR	ANCENEY MADISON V. GALLATIN CO., MT	KEENESAW OGALLALA NE CO	'L. SNAKE CR OLCOTT SIOUX CO, NE	KLEINF. FM. WOOD MT. S. SASKATCH	CUNNINGHAM COLTER TETON CO, WY
CLAREN- DONIAN											
BARSTOVIAN	LATE		<i>P. oregonensis</i> Shotwell, 1967b	<i>P. oregonensis</i> Shotwell, 1967b	<i>P. oregonensis</i> Gazin, 1932		<i>P. cf. rusticus</i> Sutton, 1977	<i>P. sp.</i> Galbreath, 1953		<i>P. borealis</i> ● Storer, 1975	<i>P. sp.</i>
	EARLY	<i>P. sp.</i> Lindsay, 1972				<i>P. cf. oregonensis</i> Downs, 1956			<i>P. rusticus</i> ● Matthew, 1924 Skinner et al., 1977		
HEMING- FORDIAN											

Fig. 19.—Geographic and stratigraphic range of *Peridiomys*.

Table 9.—Dental measurements, *Peridiomys*, Colter Formation.

Tooth	Specimen	AP	TA	TP	AP/T	Locality
<i>Lower Teeth</i>						
M ₁ or 2	UWBM 62676	1.2	1.4	1.3	0.86	North Pilgrim 2
M ₁ or 2	UWBM 62664	1.2	1.4	1.4	0.86	North Pilgrim 2
M ₁ or 2	KUVP 17496	1.3	1.4	1.4	0.93	Cunningham Hill
M ₃	UWBM 62683	1.0	1.1	1.0	0.91	North Pilgrim 2
<i>Upper Teeth</i>						
M ¹ or 2	UWBM 62638	1.1	1.6	1.5	0.69	North Pilgrim 2
M ¹ or 2	UWBM 62648	1.0	1.3	1.2	0.77	North Pilgrim 2

Description and comparison.—Lower molars of *Peridiomys* from Jackson Hole (Pl. IV M, N) are smaller than those of *P. rusticus* and *P. cf. P. rusticus* (Fig. 19), in which measurement T exceeds 1.7 mm. The sizes of the Jackson Hole teeth fall within the range for *P. oregonensis* and probably within that for *P. borealis*. The following UWBM and KUVP specimens from Jackson Hole are nearly identical to previously described and figured teeth of *P. oregonensis* from Red Basin: UWBM 62664 to UO 22877 (Shotwell, 1967b:fig. 9a), and KUVP 17496 to UO 24207 (Shotwell, 1967b:fig. 9c). M₃ has two roots, with the anterior one the most prominent.

M¹–M² from Jackson Hole most closely resemble specimens of *P. cf. P. oregonensis* from the Mascall fauna in size. The type of *P. oregonensis* is slightly larger. In occlusal pattern, an unworn specimen from Jackson Hole (Pl. IV O, P) also resembles an M¹ of

P. cf. P. rusticus from Anceney (CMNH 27908). The protocone protrudes just posterior to the protostyle and paracone, which connect by a prominent anterior cingulum. On the metaloph, slight posteriad offset of the hypocone causes minor curvature of the loph and no posterior cingulum is present. With wear, the lophs join lingually to form a horseshoe shape, and in extreme wear a uniformly wide band of enamel surrounds a single dentine field. Three roots are well developed, with the labial two beginning to bifurcate 0.2 mm below the enamel-dentine border.

Discussion.—The molars of *Peridiomys* from Jackson Hole are too small to be assigned to *P. rusticus* or *P. cf. P. rusticus*. The size of the teeth from Jackson Hole resembles that in *P. oregonensis*, *P. cf. P. oregonensis*, and *P. borealis*. In occlusal pattern, teeth from Jackson Hole are nearly identical

		RANGE OF <i>DIPRIONOMYS</i>										● TYPE LOCALITY
FAUNA		LITTLE VALLEY	BLACK BUTTE	THOUSAND CRK.	FISH LAKE V.	NORDEN BR.	ANNIES GCO.	DEVILS GULCH	BURGE	KLEINF. FM.	CUNNINGHAM	
FM		MALHEUR CO. OR.	MALHEUR CO. OR.	HUMBOLDT CO. NV.	ESMERALDA CO. NV.	VALENTINE	VALENTINE	VALENTINE	VALENTINE	WOOD MT.	COLTER	
LOCATION		CO. OR.	CO. OR.	CO. NV.	CO. NV.	BROWN CO. NB.	KNOX CO. NB.	BROWN CO. NB.	BROWN CO. NB.	S. SASKATCH.	TETON CO. WY.	
HEMPHILLIAN		<i>D. parvus</i> Shotwell, 1967b	<i>D. sp.</i> Shotwell, 1967b	<i>D. parvus</i> ● Wood, 1935								
CLARENDONIAN	LATE											
	EARLY				<i>D. cf. D. parvus</i> Clark et al., 1964				<i>D. agrarius</i> Webb, 1969			
BARSTOVIAN	LATE					<i>D. agrarius</i> Klingener, 1968	<i>D. agrarius</i> Korth, 1979	<i>D. agrarius</i> ● Wood, 1935		<i>D. cf. agrarius</i> Storer, 1975	<i>D. agrarius</i>	

Fig. 20.—Geographic and stratigraphic range of *Diprionomys*.

Table 10.—Dental measurements, *Diprionomys agrarius*, Colter Formation.

Tooth	Specimen	AP	TA	TP	AP/T	Locality
<i>Lower Teeth</i>						
P ₄	UWBM 62660	1.4	1.2	1.4	1.00	North Pilgrim 2
M _{1 or 2}	UWBM 62671	1.4	1.6	1.4	0.88	North Pilgrim 2
M ₃	UWBM 62275	1.3	1.6	—	0.81	North Pilgrim 2
M ₃	UWBM 62677	1.2	1.4	—	0.86	North Pilgrim 2
<i>Upper Teeth</i>						
M ¹ or 2	UWBM 62626	1.3	1.7	1.5	0.76	North Pilgrim 2
M ¹ or 2	UWBM 62630	1.0	1.6	1.3	0.63	North Pilgrim 2
M ¹ or 2	UWBM 62631	1.3	1.6	1.4	0.81	Cunningham Hill
M ¹ or 2	UWBM 62769	1.2	1.5	1.4	0.80	Cunningham Hill
M ¹ or 2	UWBM 62772	1.2	1.5	1.4	0.80	Cunningham Hill

to those of *P. oregonensis*. Teeth in similar wear stages have not been reported for other species, thus precluding species identification.

Genus *Diprionomys* Kellogg, 1910

Diprionomys agrarius Wood, 1935

Plate II D–H

Proheteromys Sutton and Black (1972), in part.

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Fig. 20.

Referred specimens.—P₄, UWBM 62660. M₁ or M₂, UWBM 62671. M₃, UWBM 62675, 62677. P⁴, KUVF 17499. M¹ or M², UWBM 62626, 62630, 62631, 62722. M², UWBM 62769. UWBM 62769, 62772, and KUVF 17499 from Cunningham Hill, others from North Pilgrim 2.

Measurements.—Table 10 and Wood (1935), Korth (1979), Klingener (1968), Storer (1975), Shotwell (1967b), Clark et al. (1964), Barnosky (1983).

Description and comparison.—The P₄ is more worn than that of the type specimen for *D. agrarius*, but similar in general morphology. At least three cusps form the metalophid, with the labial one joining the hypolophid in late wear (Pl. II F). Lingually, the metalophid barely touches the hypolophid and isolates a central basin. At a similar stage of wear, the same condition would prevail in all *Diprionomys* that I have seen. The size of the P₄ from Jackson Hole most closely approximates that of *Diprionomys agrarius* from Norden Bridge and Knox County. As in the type of *D. agrarius*, the roots fuse for at least 1 mm below the base of the crown, where they are broken off.

Like the condition in *Diprionomys agrarius*, in which four M₁₋₂'s average 1.4 mm AP, the size of

lower molars from Jackson Hole exceeds that of *D. parvus*, in which lower (n = 5) and upper (n = 4) M₁₋₂'s average 1.1 mm AP (Wood, 1935; Shotwell, 1967b; Clark et al., 1964). Although wear has removed cusps from the Jackson Hole specimens, the general outline of the lophids in UWBM 62671 (Pl. II E) closely approximates that in the type of *D. agrarius*.

M₃'s from Jackson Hole (Table 10) are not much smaller than the M₁ or 2. They about equal P₄ in width, as Wood (1935:179) noted for the type of *D. agrarius*. The M₃ from Knox County was found to be wider than the P₄ (Korth, 1979:302). Equally wide anterior and posterior lophids connect to a single simple root in the teeth from Jackson Hole, as Shotwell also described for *D. parvus*.

The single fragment of P⁴ shows a transversely elongate but essentially single cusped photoloph that connects to the entostyle via a short ridge. Connection is much less prominent than in *D. parvus* and the protoloph is much narrower. The entostyle, which is considerably more anterior with respect to the metaloph than in *D. parvus*, nearly aligns with the protoloph. The entostyle in *D. parvus* is located well posterior of the protoloph, although it is still the most anterior cusp on the metaloph. Judging from figures in Clark et al. (1964), the entostyle in a P⁴ from the Esmeralda Formation occurs farther posterior than in the Jackson Hole specimen, but farther anterior than in *D. parvus*. The width of the tooth from Jackson Hole (1.55 mm minimum) exceeds that of *D. cf. D. agrarius* from the Wood Mountain Formation (1.3 mm, mean of 7 specimens, OR = 1.13–1.41 mm, Storer, 1975) or *D. cf. D. parvus* (1.43 mm, Clark et al., 1964). It is narrower, however, than in *D. agrarius* from Knox County (1.78 mm, mean of 4 specimens, OR = 1.62–

		RANGE OF <i>LIGNIMUS</i>						● TYPE LOCALITY
FAUNA FM LOCATION		NIOBRARA R. VALENTINE CHERRY CO., NB	NORDEN BR VALENTINE BROWN CO., NB	ANNIES GCO VALENTINE KNOX CO., NB	BURGE VALENTINE BROWN CO., NB	WAKEENEY OGALLALA TREGO CO., KS	KLEINF. FM. WOOD MT. S. SASKATCH	CUNNINGHAM COLTER TETON CO., WY
HEMPHILLIAN								
CLARENDONIAN	LATE					<i>L. hibbardi</i> ● Storer, 1973		
	EARLY				<i>L. sp.</i> Storer, 1973			
BARSTOVIAN	LATE	<i>L. sp.</i> Storer, 1973	<i>L. sp.</i> <i>L. cf. montis</i> Storer, 1973	<i>L. cf. hibbardi</i> Korth, 1979			<i>L. montis</i> ● Storer, 1973 1975	<i>L. transversus</i> ● new species

Fig. 21.—Geographic and stratigraphic range of *Lignimus*.

1.87, Korth, 1979), and falls near the average for *D. parvus* from Little Valley (1.49 mm, mean of 5 specimens, OR = 1.18–1.74, Shotwell, 1967b).

Upper molars were hitherto unknown for *D. agrarius*. One Jackson Hole M² is virtually unworn and shows that three transversely aligned cusps compose each of the loph. The loph lack anterior and posterior cingula. The protocone is anteroposteriorly compressed, flattened anteriorly, and aligns almost exactly with the protostyle and paracone. The protocone nearly touches the protostyle, but a notch separates it from the paracone. On the meta-loph, the hypocone occurs slightly posterior to the entostyle and metacone, and a ridge of enamel connects all three cusps. *D. parvus* from Little Valley (UO 26014) differs in the more pronounced cingula, which would be expected if the tooth is an M¹ rather than M².

Worn M¹–M² from Jackson Hole (Pl. II D) are horseshoe shaped because the protoloph and meta-loph fuse lingually, as also occurs in *D. parvus*. Unlike *D. parvus*, lophs in the Jackson Hole specimens do not join labially to isolate a central lake. In upper molars from Jackson Hole, enamel on the most posterior band is only about half as thick as on the rest of the occlusal surface (Pl. II D). This contrasts with two illustrations of *D. parvus* where enamel slightly thins anteriorly (UO 26004) or is of about equal width (UO 26024) throughout. A third tooth of *D. parvus* shows posterior thinning of the enamel (UO

26022) (Shotwell, 1967a). In labial view, roots on the Jackson Hole M¹–M²'s fuse for about 0.7 mm above the crown, with the remaining unfused portion measuring about 1.0 mm. In contrast, the fused portion of the root is longer than the unfused portion in *D. parvus* (UO 26014).

Discussion.—Teeth from Jackson Hole do not differ significantly from the type of *Diprionomys agrarius* or the Norden Bridge material. Small samples suggest that individuals of *D. agrarius* from the Knox County, Nebraska, locality were probably larger but of the same species. Cheek teeth of *D. agrarius* are less hypsodont than in *D. parvus*, shown by greater fusion of roots and labial closure of the transverse valley in upper molars of *D. parvus*. Labial closure is accomplished by development of a labial enamel ridge between the two lophs. The Jackson Hole material and other *D. agrarius* also differ from *D. cf. D. parvus* in larger size.

Korth (1979) suggested that *D. parvus* from Little Valley and Thousand Creek (Fig. 20) represents a genus other than *Diprionomys*. Of the characters that I have seen, the configuration of P⁴ may support that conclusion, but samples of the commonly variable tooth are very small. I include *D. parvus* in *Diprionomys*, while recognizing the possibility that *D. parvus* is phylogenetically more distant from *D. agrarius* than is *D. cf. D. parvus*, as Korth (1979) suggested. *D. cf. D. agrarius* from the Wood Mountain Formation, because of its small size, may rep-

resent a distinct species more closely related to *D. agrarius*, but more material is needed for accurate diagnosis.

Genus *Proheteromys* Wood, 1932

Proheteromys, species indeterminate

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range.—Arikareean through Barstovian of North America.

Referred specimens.—P⁴, KUVF 17807.

Discussion.—The small, worn P⁴ measures 1.0 (AP) × 1.0 mm (T), is brachyodont, and shows a protoloph joined to the entostyle as is typical of *Proheteromys*. Species diagnosis is not possible.

Family Geomyidae Gill, 1872

Subfamily uncertain

Genus *Lignimus* Storer, 1970

Lignimus transversus, new species

Plate V

Proheteromys Sutton and Black (1972), in part.

Holotype.—UWBM 62662, right M₁ or M₂.

Hypodigm.—UWBM 62655 (P₄), 62663, 62666, 62668, 62669, 62681 (M₁ or M₂), 62686, 62687 (M₃), 62616 (P⁴), 62611, 62621, 62624, 62629, 62634, 62635 (M¹ or M²), 62644, 62645 (M³).

Type Locality.—North Pilgrim 2, UWBM loc. C0237.

Etymology.—"Transversus" referring to transversely straight anterior margin of hypolophid.

Age.—Late Barstovian.

Range of genus.—Fig. 21.

Referred specimens.—P₄, UWBM 62652, 62758. M₁ or M₂, UWBM 62782, 62785. M₃, UWBM 62779, 62781, KUVF 17495. P⁴, UWBM 62760. M¹ or M², UWBM 62768, 62771, 62777, KUVF 17490. UWBM 62652 from type locality, others from Cunningham Hill, loc. C0236.

Measurements.—Table 11 and Storer (1973, 1975), Korth (1979), and Barnosky (1983).

Diagnosis.—Cheek teeth brachyodont, roots present, dentine tracts absent. P₄ with two cusps on metalophid (versus three or four in *L. montis*), ratio AP/T more than 1.0. M₁–M₂ with prominent anterolabial lake, V shaped lophs, ratio of AP/T ranging from about 0.76 to 0.89, hypolophid anteriorly flatter than in *L. montis*. M₃ with ratio of AP/T generally between 0.85 and 0.93, connection between metalophid and hypolophid not pronounced.

P⁴ with ratio AP/T less than 1.00, single cusp usual on protoloph. M¹–M² with relatively bulbous cusps, ratio AP/T usually between 0.70 and 0.75. Molars larger than in *L. montis*, with average AP of M₁ and M₂ = 1.46 mm (versus 1.26 mm in *L. montis*), average AP of M¹ and M² = 1.28 mm (versus 1.14 mm).

Description and comparison.—The cheek teeth from Jackson Hole are relatively brachyodont and lack dentine tracts (Pl. V). Teeth of *L. montis* are similar in these respects. *L. sp.* (Fig. 21) and *L. cf. L. hibbardi* have tracts that reach about half the height of the molar crown. In *L. hibbardi*, tracts are two-thirds as high as the crown. M₁ and M₂ of *L. transversus* (Pl. V F) and *L. montis* have roots; these teeth lack roots in *L. cf. L. hibbardi* and *L. hibbardi*. In P₄ of *L. transversus*, the protoconid-metaconid complex forms a single cusp that is separated from the protostylid by a slight anterior notch (Pl. V B). In contrast, at least three prominent cusps make the metalophid of *L. montis*, with the most anterior one forming a projection in the same area as the notch occurs in *L. transversus* (compare Pl. V B with fig. 75A, B in Storer, 1975). Where P₄ is known, other *Lignimus* resemble *L. montis* in this respect. The hypolophid in *L. transversus*, as in all species, is composed mainly of two transversely aligned cusps, the hypoconid and entoconid. The hypostylid in *L. transversus* is rudimentary. P₄ of *L. transversus* is slightly narrower than the single comparative specimens of *L. montis* and *L. hibbardi* (ratio AP/T = 1.0), but wider than the average of 11 teeth of *L. cf. L. hibbardi* (mean, ratio AP/T = 1.15) (Korth, 1979; Storer, 1973, 1975; and Table 11). P₄ of *L. transversus* is about 10% smaller than in *L. montis*, and 10%–20% smaller than in *L. cf. L. hibbardi* and *L. hibbardi*.

M₁–M₂ of *L. transversus* (Pl. V A, C–H) closely resemble those of *L. montis*, which Storer (1975) described in detail. The protoconid and metaconid, which are set relatively far posterior of the anterior border of the tooth, are prominent (Pl. V C). Ridges project anteromedially from the center of each cusp and meet near the center of the anterior border. They thus form a rostrally pointing V. A posterior V, formed by ridges extending off the entoconid and hypoconid, parallels the anterior one. This posterior V is considerably more prominent in worn teeth of *L. montis* than in *L. transversus*. A prominent anterolabial cingulid runs from a minute protostylid to the apex of the anterior V and, in concert with the protoconid, borders a lake that forms as the

Table 11.—*Dental measurements, Lignimus transversus, new species, Colter Formation.*

Tooth	Statistic* or Specimen	AP	TA	TP	AP/T	Locality
P ₄	UWBM 62655	1.6	1.3	1.5	1.07	NP
	UWBM 62652	—	1.2	—	—	NP
	UWBM 62758	1.6	1.2	1.5	1.07	CH
M ₁ or M ₂	Mean	1.46	1.74	1.73	0.83	NP and CH
	SD	0.172	0.152	0.206	0.045	
	OR	1.3–1.7	1.6–2.0	1.5–2.1	0.76–0.89	
	N	7	5	7	6	
M ₃	Mean	1.20	1.30	1.16	0.90	NP and CH
	SD	0.071	0.071	0.055	0.039	
	OR	1.1–1.3	1.2–1.4	1.1–1.2	0.85–0.93	
	N	5	5	5	5	
P ⁴	UWBM 62616	1.5	0.9	1.8	0.83	NP
	UWBM 62759	1.7	1.1	1.8	0.94	CH
M ¹ or M ²	Mean	1.28	1.78	1.70	0.72	NP and CH
	SD	0.084	0.084	0.100	0.012	
	OR	1.2–1.4	1.7–1.9	1.6–1.8	0.71–0.74	
	N	5	5	5	5	
M ³	UWBM 62644	1.4	1.6	—	0.88	NP
	UWBM 62645	1.3	1.5	—	0.87	NP

* See Barnosky (1983) for measurements of individual specimens and summary of measurements of other species.
NP North Pilgrim 2.
CH Cunningham Hill.

tooth wears (Pl. V D). Other species differ from *L. transversus* and *L. montis* in their flattening of the V's to form two straight lophs, and poor development or absence of an anterolabial enamel lake. The M₁'s and M₂'s in *L. montis* and *L. transversus* are relatively narrow, with the ratio of AP/T averaging 0.81 and 0.83, respectively. The ratios of AP/T are smaller, meaning wider teeth, in *L. cf. L. hibbardi* (OR of ratio AP/T = 0.70–0.75, n = 2) and *L. hibbardi* (OR = 0.62–0.68, n = 2).

M₃ of *L. transversus* (Pl. V I, J) resembles that in *L. montis* except for two major features. In *L. transversus*, the anterolabial enamel lake is more transient and the central connection between the metalophid and hypolophid is less pronounced. Lophids, as well as length of the tooth, are more compressed in the Burge *L. sp.* (ratio AP/T = 0.56, n = 1), *L. cf. L. hibbardi* (AP/T = 0.76, n = 1), and *L. hibbardi* (AP/T = 0.75–0.78, n = 2). UWBM 62779 possesses a single large root.

P⁴ of *L. transversus* (Pl. V K, L, O, P), like that of all the species, is composed of a three cusped metaloph. The protoloph is composed of a single transversely ovoid cusp in all species. Some specimens of *L. montis* possess an extra cusp anterad to the protoloph. With wear, the protoloph joins the metaloph just lingual of center as in all species in which P⁴ is known. Unworn cusps on the metalophid are slightly bulbous, especially the hypocone

(Pl. V K). A weak posterior cingulum joins the hypocone to the entostyle, which is compressed transversely. Unworn P⁴'s of other species have not been reported. Like *L. hibbardi*, *L. cf. hibbardi*, and Cherry Co. *L. sp.*, *L. transversus* has a short P⁴ in which the ratio AP/T < 1.00. *L. montis* and the Norden Bridge *L. sp.* have a longer P⁴ in which the ratio AP/T ≥ 1.05. *L. transversus* resembles *L. montis* in lacking dentine tracts. Tracts are long in *L. cf. L. hibbardi*, *L. hibbardi*, and *L. sp.*

The M¹–M² of *L. transversus* (Pl. V M, N, Q, R, U, V) are nearly identical to those in *L. montis* and *L. cf. L. montis* in occlusal pattern. In teeth tentatively identified as M¹ (Pl. V M), the protoloph consists of a moderately bulbous paracone, protocone, and protostyle, with the protocone set slightly posterior to the other two. The anterior cingulum forms about one-third the anteroposterior length of the loph. The metaloph curves slightly because the hypocone rests posterior to the metacone and entostyle. In teeth tentatively identified as M² (Pl. V Q), the anterior cingulum is at maximum about one-fifth as long as the protoloph and the protocone is even with or slightly anterior to the paracone and protostyle. Wear soon obscures these differences, and eventually joins the lophs at their lingual margin. Except for a probable M² of *L. cf. L. hibbardi* (UNSM 56343), unworn M¹–M²'s of species other than *L. montis* have not been described. UNSM

RANGE OF <i>MOJAVEMYS</i> • TYPE LOCALITY					
FAUNA FM	BARSTOW	BARSTOW	QUARTZ B. DEER BUTTE MALHEUR CO., OR	MASCALL " N. CENTRAL OR	CUNNINGHAM COLTER TETON CO., WY
LOCATION	SAN BERNARDINO CO., CA				
CLAREN-DONIAN					
BARS TOVIAN	LATE	<i>M. lophatus</i> Lindsay, 1972	<i>M. alexandrae</i> Lindsay, 1972	<i>M. mascallensis</i> Shotwell, 1967 b	<i>M. magnumarcus</i> new species
	EARLY	<i>M. lophatus</i> Lindsay, 1972	<i>M. alexandrae</i> Lindsay, 1972	<i>M. mascallensis</i> Downs, 1956	
HEMING-FORDIAN					

Fig. 22.—Geographic and stratigraphic range of *Mojavemys*.

56343 and slightly worn specimens of *Lignimus* sp. and *L. cf. L. hibbardi*, however, suggest that the cusps are transversely more flattened and anterior cingula less pronounced than in *L. transversus*. M¹–M² of *L. transversus* are slightly longer than in *L.*

cf. L. hibbardi (average ratio AP/T = 0.66, OR = 0.60–0.71, n = 5), but on the average slightly shorter than in *L. montis* (average AP/T = 0.76, OR = 0.69–0.87, n = 13), *L. cf. L. montis* (average AP/T = 0.80, n = 4), and possibly *L. hibbardi* (average AP/T = 0.74, OR = 0.70–0.78, n = 2) (Table 11).

Two M³'s (Pl. V S, T) of *L. transversus* are known but are too worn for meaningful comparison. The loph join lingually and after extreme wear enclose a central lake. Like all molars of *L. transversus*, M³'s are from 10%–30% larger than in *L. montis*.

Discussion.—The main evolutionary trends in *Lignimus* seem to be (1) straightening of the V shaped lophids in M₁–M₂, (2) compression of the cheek teeth anteroposteriorly, (3) increasing hypsodonty, and (4) development of dentine tracts. In all of these charaters, *L. transversus* resembles the most primitive species, *L. montis*, most closely. Less prominent V's on the hypolophids suggest that *L. transversus* is slightly more advanced than *L. montis* and morphologically closer to the stock that gave rise to later species of *Lignimus*.

Table 12.—Dental measurements, *Mojavemys magnumarcus*, new species, Colter Formation.

Tooth	Statistic* or Specimen	AP	TA	TP	AP/T	Locality
P ₄	UWBM 62661	1.7	1.1	1.6	1.06	NP
	UWBM 62765	1.6	1.0	1.2	1.33	CH
M ₁	Mean	1.57	1.82	1.78	0.85	
	SD	0.137	0.160	0.098	0.024	NP and CH
	OR	1.5–1.8	1.7–2.1	1.7–1.9	0.82–0.88	
	N	6	6	6	6	
M ₂	UWBM 62665	—	1.9	—	—	NP
	UWBM 62766	1.4	1.8	1.7	0.78	CH
	UWBM 62783	1.4	1.8	1.8	0.78	CH
	KUVP 17491	1.4	1.7	1.7	0.82	CH
M ₃	Mean	1.22	1.40	1.10	0.88	NP and CH
	SD	0.103	0.149	0.156	0.095	
	OR	1.1–1.4	1.2–1.7	0.9–1.4	0.73–1.08	
	N	10	10	10	10	
P ⁴	UWBM 62617	1.7	—	1.8	0.94	NP
	UWBM 62760	—	—	1.8 ^a	—	CH
	UWBM 62776	—	—	1.9 ^a	—	CH
	UWBM 62778	—	—	1.9	—	CH
M ¹ or M ²	Mean	1.43	1.81	1.70	0.79	NP
	SD	0.052	0.146	0.141	0.060	
	OR	1.4–1.5	1.7–2.1	1.5–1.9	0.71–0.88	
	N	6	7	6	6	
M ³	UWBM 62646	1.1	1.4†	—	0.79	NP
	UWBM 62647	1.1	1.3†	—	0.85	NP
	KUVP 17498	1.2	1.6†	—	0.75	NP

* See Barnosky (1983) for measurements of individual specimens and summary of measurements of other species.

† Measurement T.

NP North Pilgrim 2.

CH Cunningham Hill.

^a approximately.

Genus *Mojavemys* Lindsay, 1972*Mojavemys magnumarcus*, new species

Plate VI

Proheteromys Sutton and Black (1972) in part.

Holotype.—UWBM 62641, M¹ or M².

Hypodigm.—UWBM 62667, 62665 (M₂) from type locality.

Type locality.—North Pilgrim 2, UWBM loc. C0237.

Etymology.—Magna (large), arcus (arch) refers to large size and prominent, arch-shaped basal chevron of upper molars.

Age.—Late Barstovian.

Range of genus.—Fig. 22.

Referred specimens.—From UWBM loc. C0237, P₄, UWBM 62661, M₁, UWBM 62673, M₃, UWBM 62678, 62679, 62680, 62682, 62684, 62689, 62690, 62691, P⁴, UWBM 62617, M¹ or M², UWBM 62622, 62623, 62627, 62636, 62637, 62643, 62649, M³, UWBM 62646, 62647.

From UWBM loc. C0236, P₄, UWBM 62765, M₁, UWBM 62770, 62780, 62784, 62786, M₂, UWBM 62783, 62766, KUVF 17491, M₃, UWBM 62773, 62775, KUVF 17493, P⁴, UWBM 62759, 62776, 62778, M³, UWBM 62767, KUVF 17498.

Measurements.—Table 12 and Lindsay (1972), Downs (1956), Shotwell (1967a), Barnosky (1983).

Diagnosis.—P₄, M₁, M₂, M¹, M², M³ from 10%–30% larger than in *M. lophatus* or *M. mascallensis*. M₂ with transversely elongate metaconid, prominent anterolabial cingulid extending anterior to protoconid, cusps with more pronounced anteroposterior compression than in other species. M¹–M² with well developed enamel chevron at lingual base, ratio CHEV/T exceeding 0.30.

Description and Comparison.—Cusp morphology in P₄ of *M. magnumarcus* (Pl. VI A, C) approximates the morphology in *M. mascallensis* (UO 22740). Three cusps make the metalophid, with the middle one most anterior and very prominent. A short, anteroposteriorly oriented crest connects the metalophid and hypolophid. The hypolophid is compressed anteroposteriorly. Individual variation among the P₄'s of *M. magnumarcus* is apparently marked, as in *M. lophatus* (Table 12). Wear stage accounts for only part of the variation in the ratio of AP/T for the Jackson Hole P₄'s. With continued wear, the occlusal pattern in UWBM 62765 would approximate the pattern in the type specimen of *M. lophatus*, but the posterior border would bulge less than in *M. mascallensis*. In a worn P₄ of *M. magnumarcus* (UWBM 62661), the metalophid expands anteriorly more than in known specimens of *M.*

lophatus or the type of *M. mascallensis* (UCMP 39094), but resembles *M. mascallensis* from the Quartz Basin (UO 22740 and LACM CIT 4002b). The posterior margin of the hypolophid, bulging more than in *M. lophatus*, approximates the condition in *M. mascallensis*. In *M. magnumarcus* one anterior root is preserved and is distinctly separated from the posterior roots. Separate anterior and posterior roots are also present in *M. mascallensis*.

The general morphology of M₁–M₂ in *Mojavemys magnumarcus* (Pl. VI B, D, E, F–M) closely follows that described by Lindsay (1972) for *M. lophatus* and by Shotwell (1967a) and Downs (1956) for *M. mascallensis*. The anterolabial cingulid of M₁ (Pl. VI B), as in *M. lophatus*, trends anteroposteriorly and extends only one third of the way across the metalophid. In *M. mascallensis* (UO 22736), the cingulid trends more transversely, and extends about half of the way across the metalophid. One anterior and one posterior root fuse near the base of the crown (as in Pl. VI L), but diverge widely ventrad like those in *M. lophatus*. Two anterior and two posterior roots, all separate, are present in *M. mascallensis*.

The M₂ in *M. magnumarcus* has an anterolabial cingulid that extends about half way across metalophid as in *M. alexandrae* and *M. lophatus*. The two M₂'s that are nearly unworn, UWBM 62766 (Pl. VI D) and 62665, differ from unworn teeth of *M. alexandrae* and *M. lophatus* in the transversely wider, more lophate metaconid, and more pronounced anteroposterior compression of the lophids. These teeth also differ from *M. alexandrae* in having a more prominent anterior cingulid. The single anterior and single posterior root of *M. magnumarcus*, as in all species, separate distally (Pl. VI L). In the Jackson Hole specimen, as in *M. alexandrae*, the lateral sulcus on the lower teeth does not persist to the base of the crown and the enamel is thick, commonly between 0.10 and 0.15 mm.

The M₃ (Pl. VI E) contains two major anteroposteriorly compressed cusps on the metalophid, and two on the hypolophid. Both lophids are transversely straight. The rudimentary protostylid in some specimens connects to an anterolabial cingulum that extends from one third to one half way across the metalophid. The pattern is nearly identical in *M. alexandrae*, the only other species for which unworn M₃'s are reported. With considerable wear, lophids join labially in *M. magnumarcus*. Two roots, one anterior and one posterior, curve markedly poste-

Table 13.—Measurements, hypsodonty, *Mojavemys magnumarcus*, new species, and other species of genus.

Tooth	Specimen	TOTH*	CHEV	T	LINH/T	CHEV/T	TOTH/T
<i>Mojavemys alexandrae</i>							
M ²	UCMP 78156	1.4	0.5	1.9	0.74	0.26	1.00
M ²	UCMP 78157	—	0.4	1.8	—	0.22	—
<i>Mojavemys lophatus</i>							
M ¹	UCMP 78162	1.2	0.9	1.85	0.65	0.49	0.92
M ²	UCMP 78137	0.9	0.4	1.3	0.69	0.31	1.00
<i>Mojavemys magnumarcus</i>							
M ¹ or 2	UWBM 62627	1.1	—	1.7 mx	0.65	—	—
M ¹ or 2	UWBM 62641	1.0	0.7	1.7	0.58	0.41	1.00

* See Fig. 16 for explanation of measurements.
mx maximum.

rad. The anterior one is rudimentary and in some specimens is fused to the posterior one.

The samples of P⁴ are small for all species. In the Jackson Hole material, the protoloph is formed by a single, transversely elongate cusp (Pl. VI O, P). With wear, the protoloph joins lingually to the metaloph. The same condition prevails in all *Mojavemys*.

The M¹–M²'s from Jackson Hole (Pl. VI Q) are too worn to display details of the cusps, but resemble similarly worn specimens of *M. alexandrae* in proportions. They are anteroposteriorly shorter than teeth of *M. mascallensis* (ratio AP/T = 0.93–1.00, n = 2). Teeth of *M. magnumarcus* are on average

15% larger than those of *M. lophatus* (AP = 0.9–1.2 mm, n = 4) and 20% larger than in *M. mascallensis* (AP = 0.9–1.0 mm, n = 2). The lingual chevrons in *M. magnumarcus* (Pl. VI T) are higher than in *M. alexandrae* (Table 13, Fig. 16). The lophs in *M. magnumarcus*, like in *M. lophatus*, are slightly more compressed anteroposteriorly than in *M. alexandrae*.

The M³ (Pl. VI R, S), as in *M. lophatus* and *M. alexandrae*, possesses a central basin that is ringed by the protoloph and metaloph. In contrast, the central basin opens labially in *M. mascallensis*. Like the condition in *M. lophatus*, the only other taxon

RANGE OF COPEMYS

FAUNA FM LOCATION	BARSTOW	BARSTOW	AVAWATZ	MATTHEWS RCH CALIENTE	NETTLE SPRING CALIENTE	DOMES SPRING CALIENTE	RED BASIN BUTTE CRVS	QUARTZ B. DEER BUTTE	BLACK BUTTE JUNTURA	LITTLE VALLEY	BARTLETT MT. HARNEY CO., OR	MC KAY UMATILLA CO., OR
	SAN BERNADINO CO. CALIFORNIA			CUYAMA VALLEY, CALIFORNIA			MALHEUR CO. OREGON					
HEMPHILLIAN											<i>C. esmeraldensis</i>	Shotwell, 1967a Lindsay, 1972
CLARENDONIAN	LATE				<i>C. russelli</i> James, 1963					<i>C. dentalis</i> <i>C. esmeraldensis</i> Shatwell & Russell, 1963 Lindsay, 1972		
	EARLY		<i>C. dentalis</i> Wilson, 1939	<i>C. russelli</i> • James, 1963								
BARSTOVIAN	LATE	<i>C. pagei</i> <i>C. tenuis</i> • <i>C. russelli</i> <i>C. esmeraldensis</i> Lindsay, 1972	<i>C. langidens</i> • <i>C. barstowensis</i> • Lindsay, 1972			<i>C. aff. C. dentalis</i> James, 1963	<i>C. pagei</i> Shatwell, 1967a	<i>C. pagei</i> • Shatwell, 1967a				
	EARLY	<i>C. pagei</i> Lindsay, 1972										
HEMINGFORDIAN												

Fig. 23.—Geographic and stratigraphic range of *Copemys* in California and Oregon.

RANGE OF *COPEMYS*

FAUNA FM LOCATION	● TYPE LOCALITY									
	FISH LAKE V. ESMERALDA CO., NV	ANCENEY MADISON V. GALLATIN CO., MT	'SANTA FE' NEW MEXICO	REDINGTON QUIBURIS REDINGTON, AZ	NIOBRARA R. VALENTINE CHERRY CO, NB	NORDEN BR VALENTINE BROWN CO, NB	ANNIES GCO VALENTINE KNOX CO, NB	WAKEENEY OGALLALA TREGO CO, KS	KLIENF. FM WOOD MT. S. SASKATCH	CUNNINGHAM COLTER TETON CO, WY
HEMPHILLIAN				<i>C. vasquezii</i> ● Jacobs, 1977						
CLARENDONIAN	LATE							<i>C. shotwellii</i> ● <i>C. pisinnus</i> ● Wilson, 1968		
	EARLY	<i>C. dentalis</i> ● <i>C. esmeraldensis</i> ● Hall, 1930 Clark et al., 1964		↑ ? <i>C. loxodon</i> ● Wood, 1936						
BARSTOVIAN	LATE	<i>C. sp.</i> Sutton, 1977	Clark and others, 1964 ?		<i>C. niobrariensis</i> ● <i>C. kelloggae</i> ● Hoffmeister, 1959	<i>C. kelloggae</i> Klingener, 1968	<i>C. kelloggae</i> Korth, 1980		<i>C. kelloggae</i> Storer, 1975	<i>C. kelloggae</i>

Fig. 24.—Geographic and stratigraphic range of *Copemys* east of California and Oregon.

for which an unworn M³ is known, the protocone is the only prominent cusp.

The sizes of all cheek teeth from Jackson Hole most closely resemble the sizes in *M. alexandrae*. Most M₁'s and M₂'s are slightly larger in the Jackson Hole species and the P⁴'s are 20% smaller, but the differences are not statistically significant.

Discussion.—Chevron height has been shown to increase with time in *Entoptychus*, a geomyoid genus whose general molar pattern resembles that of *Mojavemys* (Rensberger, 1971). *Mojavemys magnumarcus* is therefore probably more advanced than *M. alexandrae*, a conclusion buttressed by the more lophate character of cusps in *M. magnumarcus*. The Jackson Hole species is about as advanced in these features as *M. lophatus*.

Family Cricetidae Rochebrune, 1883

Genus *Copemys* Wood, 1936

Copemys kelloggae (Hoffmeister), 1959

Plate VII A, B

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Figs. 23, 24.

Referred specimens.—M₁, UWBM 62819. Maxilla with M¹–M³, UWBM 62821.

Measurements.—M₁: AP = 1.5 mm, T = 1.1 mm. M¹: AP = 1.6 mm, T = 1.0 mm. M₂: AP = 1.2 mm, T = 0.9 mm. M₃: AP = 0.8 mm, T = 0.8 mm. See also Hoffmeister (1959), Klingener (1968), Korth (1980), Storer (1975), and Barnosky (1983).

Description and comparison.—Lindsay (1972:fig. 40) illustrated the dental terminology used here. The size of M₁'s from Barstow resembles that in *C. dentalis* (1.5 mm AP, 1.1 mm T, n = 3), *C. russelli* from Barstow (mean = 1.48 mm AP, 1.04 mm T; OR = 1.37–1.51 mm AP, 1.00–1.12 T; n = 6), *C. pagei* from Barstow (1.49 mm AP, 1.08 mm T, n = 2), and *C. kelloggae* from Cherry Co. (1.5 mm AP, 1.16 mm T, n = 1), Norden Bridge (mean = 1.47 mm AP, 1.05 mm T; OR = 1.4–1.6 mm AP, 1.0–1.2 mm T; n = 9), and Kleinfelder Farm (mean = 1.55 mm AP, 1.1 mm T; OR = 1.36–2.06 mm AP, 0.84–1.28 mm T; n = 46). The size of the M¹ from Jackson Hole falls within the size ranges of M¹'s in these same species, although it is smaller than the mean in most cases: *C. dentalis* from Black Butte (mean = 1.54 mm AP, 1.00 mm T; OR = 1.46–1.68 mm AP, 0.94–1.05 mm T; n = 9), *C. russelli* from Barstow (mean = 1.73 mm AP, 1.13 mm T; OR = 1.60–1.85 mm AP, 1.10–1.20 mm T; n = 10 AP, 12 T), *C. pagei* from Barstow (mean = 1.52 mm AP, 0.99 mm T; OR = 1.48–1.55 mm AP, 0.92–1.05 mm T; n = 2), *C. pagei* from Quartz Basin (mean = 1.63 mm AP, 1.03 mm T; OR = 1.51–1.74 mm AP, 0.93–1.15 mm T; n = 23), and *C. kelloggae* from Norden Bridge (mean = 1.75 mm AP, 1.15 mm T; OR = 1.7–1.8 mm AP, 1.1–1.2 mm T; n = 2), Annies Geese Cross Quarry (1.71 mm AP, 1.12 mm T; n = 1), and Kleinfelder Farm (mean = 1.81 mm AP, 1.21 mm T; OR = 1.58–

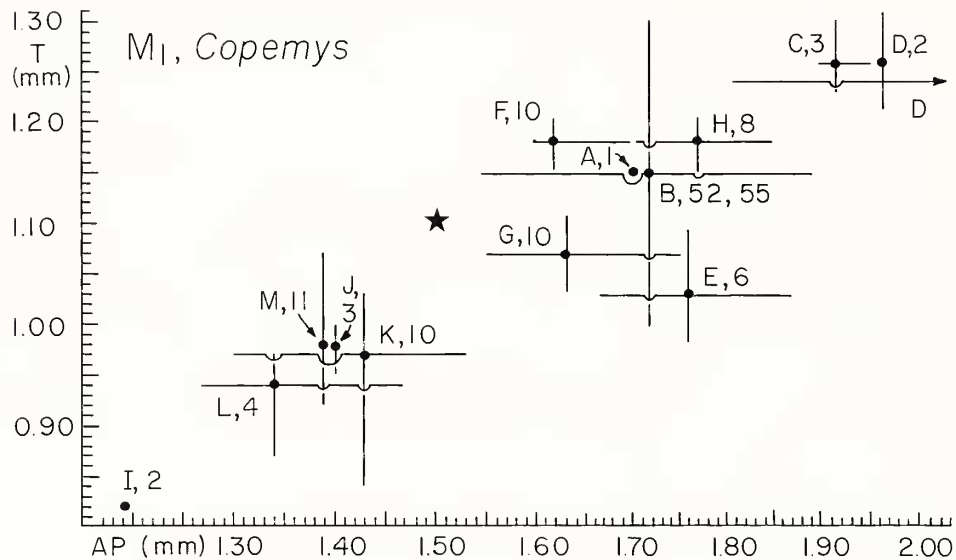


Fig. 25.—Bivariate plot of length (AP) vs. width (T) of M_1 for species of *Copemys* in which teeth are larger or smaller than teeth from Jackson Hole. Dot shows mean, lines show observed range (OR) of measurements from each locality. Numbers after letters indicate sample size; when two numbers are present the first is for AP, the second for T. Data compiled from sources listed in Figures 23 and 24. Abbreviations: *—Jackson Hole specimen. A—*Copemys loxodon* from New Mexico. B—*C. longidens*, Barstow. C—*C. esmeraldensis*, Barstow. D—*C. esmeraldensis*, Esmeralda. E—*C. esmeraldensis*, Black Butte. F—*C. russelli*, Cuyama Badlands. G—*C. tenuis*, Barstow. H—*C. barstowensis*, Barstow. I—*C. shotwelli*, Wakeeney. J—*C. pisinnus*, Wakeeney. K—*C. dentalis*, Black Butte. L—*C. vasquezi*, Redington. M—*C. pagei*, Quartz Basin. N—*C. niobariensis*, Cherry Co. Observed range of AP for J = 1.35–1.44 mm, for M = 1.26–1.53 mm; of T for D = 2.13 mm.

2.20 mm AP, 0.97–1.39 mm T; $n = 34$). The Jackson Hole teeth are smaller than teeth of *C. loxodon*, *C. longidens*, *C. esmeraldensis*, *C. russelli* from Matthews Ranch, *C. tenuis*, *C. barstowensis*, and *C. niobariensis*. They are larger than in *C. shotwelli*, *C. pisinnus*, *C. vasquezi*, and the M_1 's of *C. dentalis* from Black Butte and *C. pagei* from Quartz Basin (Figs. 25, 26).

The M_1 from Jackson Hole (UWBM 62819) (Pl. VII B) resembles specimens of *C. kelloggae* from Kleinfelder Farm, Saskatchewan, particularly ROM 6539 (Storer, 1975:fig. 58C). UWBM 62819 differs from the type of *C. kelloggae* only in the slightly less prominent and more worn hypoconulid, and more pronounced anterior cingulid. The Jackson Hole specimen is similar to referred specimens of *C. kelloggae* (UMMP 53029) (Klingener, 1968) from near the type locality in development of the anterior cingulid and hypoconulid. *C. dentalis*, *C. russelli*, and *C. pagei* lack a hypoconulid. UWBM 62819 and other *C. kelloggae* have a prominent mesolophid and ectolophid, unlike *C. dentalis* and most specimens of *C. pagei* (Shotwell, 1967a). UWBM 62819, like M_1 of *C. kelloggae*, differs from *C. russelli* in the lingually connected anteroconid and metaconid, and absence of a mesostylid. Unlike *C.*

tenuis, but resembling the condition in *C. kelloggae*, UWBM 62819 is relatively wide and has a wide anteroconid.

The anterocone of the M_1 from Jackson Hole (UWBM 62821) is bilobed (Pl. VII A). Division remains even after a moderate amount of wear. The paralophule is small but evident. The incipient, very short mesoloph is pressed against the posterior flank of the paracone. The tooth lacks a mesostyle. The metacone joins the hypocone along the tooth's posterior margin. The posterior cingulum is not prominent and merges with the metacone and hypocone after slight wear. Morphology falls within the range of variation for *C. kelloggae* from Saskatchewan (Storer, 1975) and resembles the single M_1 of *C. kelloggae* that is known from Knox County, Nebraska (Korth, 1980). UWBM 62821 differs from the Knox County tooth only in having a more prominently bilobed anterocone and a paralophule. Both of these characters commonly vary in species known by large samples. The M_1 from Jackson Hole, like the Knox County tooth, lacks a long mesoloph, whereas M_1 of *C. dentalis*, *C. russelli*, *C. pagei*, and *C. tenuis* commonly has a well developed mesoloph.

On M_2 of UWBM 62821 (Pl. VII A), the anterior cingulum is weaker lingually than on a referred M_2

of *C. kelloggae* from Knox County, Nebraska (Korth, 1980). UWBM 62821, like the Nebraska M^2 , differs from Saskatchewan specimens of *C. kelloggae* (Storer, 1975) in lacking a prominent mesoloph, and in having a narrower posterior border.

The anterior portion of M^3 of UWBM 62821 essentially resembles that of M^2 , but the anterior cingulum is slightly closer to the paracone (Pl. VII A). A shallow valley exists between the protocone and hypocone, similar to that in *C. pagei* (Shotwell, 1967a). The protocone, reduced hypocone, and metacone posteriorly border a central lake that is intermediate in size between that in illustrations of *C. pagei* and the smaller lake in *C. dentalis* (Shotwell, 1967a).

Family Eomyidae Deperet and Douxami, 1902

Genus *Pseudotheridomys* Schlosser, 1926

Pseudotheridomys cf. *P. pagei* Shotwell, 1967

Plate VII C

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of North American species.—Hemingfordian: Martin Canyon Quarry A of Logan County, Colorado (*P. hesperus* Wilson, 1960). Vedder fauna of Santa Barbara County, California (*P. cuyamensis* Lindsay, 1974). Batesland fauna of Bennett County, South Dakota (*P. sp.*, Martin, 1976). Late Barstovian: Quartz Basin and Red Basin faunas of Malheur County, Oregon (*P. pagei* Shotwell, 1967a).

Referred specimen.— P^4 or M^1 , KUVF 17486.

Measurements.—AP = 1.0 mm. T = 1.0 mm.

Description and comparison.—KUVF 17486 (Pl. VII C) differs from P^4 and M^1 in *P. pagei* mainly in its labial closure of the anterior valley. The valley remains open until late stages of wear in *P. pagei* (Shotwell, 1967a:9). The mesoloph of KUVF 17486 is long but does not quite reach the labial edge of the tooth, as in the P^4 of *P. pagei*. *P. hesperus* has a very short mesoloph. The Jackson Hole specimen more closely resembles the M^1 than the P^4 of *P. pagei* in being nearly square. In KUVF 17486 and teeth of *P. pagei*, the metaloph and mesoloph are connected, in contrast to the unconnected condition in *P. sp.* from the Batesland Formation and *P. hesperus*. *P. hesperus* usually lacks such connection in unworn teeth but the two lophs join with wear.

Discussion.—KUVF 17486 resembles teeth in *P. pagei*, except for closure of the anterior valley at an earlier stage of wear. Closure of the valley varies in *P. hesperus*, which is known by larger samples (Martin, 1976:83). The Jackson Hole species and *P. pagei* appear closely related if not conspecific. Referral of

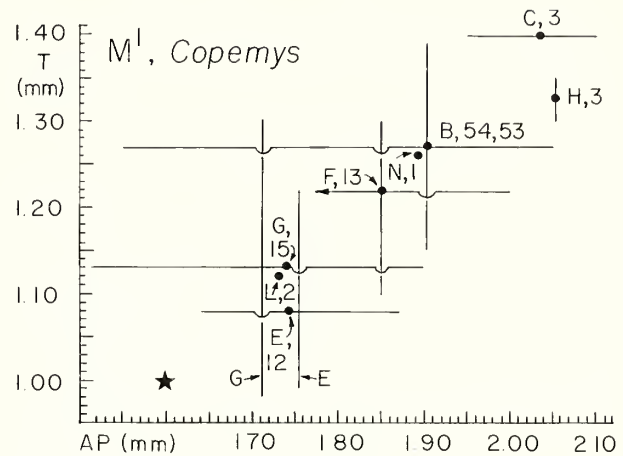


FIG. 26.—Bivariate plot of length (AP) versus width (T) of M^1 for species of *Copemys* in which teeth are larger or smaller than teeth from Jackson Hole. Observed range of AP for F = 1.10–2.00 mm. See Fig. 25 for additional explanation.

the Jackson Hole specimen is tentative because of the small sample size.

Family Zapodidae Coues, 1875

Subfamily Sicistinae Allen, 1901

Genus *Schaubeumys* Wood, 1935

Schaubeumys, species indeterminate

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Arikarean through Barstovian of Great Plains, exclusive of this occurrence. See Korth (1980) for a recent and comprehensive synopsis.

Referred specimens.— M_2 , UWBM 62726 from loc. C0237. M^1 or M^2 , KUVF 17485, UWBM 62822, 62824 from loc. C0236.

Discussion.—The referred molars from Jackson Hole show cusp morphology typical of *Schaubeumys* and *Plesiosminthus* (see Green, 1977; Black, 1958; Wilson, 1960; Engesser, 1979; Korth, 1980). Referral of the Jackson Hole material to *Schaubeumys* rather than *Plesiosminthus* is based on large size of the teeth (AP = 1.3–1.4 mm for M^1 (?)– M^2 , 1.5 mm for M_2 ; T = 1.2–1.4 mm for M^1 (?)– M^2 , 1.2 mm for M_2). Teeth of the only species of *Plesiosminthus* in North America, *P. clivosus* (Korth, 1979), are considerably smaller (AP = 1.1–1.3 mm for M^1 , 1.0–1.1 mm for M^2 , 1.1–1.2 mm for M_2 ; T = 0.9–1.2 mm for M^1 , 0.9–1.0 mm for M^2 , 0.8–1.0 mm for M_2) (Green, 1977). The nature of the Jackson Hole material combined with extreme variability within species of *Schaubeumys* (Green, 1977) precludes species assignment.

Table 14.—*Dental measurements, Parahippus tyleri, CMNH 21617, Colter Formation.*

Tooth	AP	T	C	Wear stage
<i>Upper Teeth</i>				
P or M	—	24	19	moderate
P or M	19	24	17	pronounced
<i>Lower Teeth</i>				
<i>Left ramus</i>				
P ₃	18	12	10	pronounced
P ₄	17	12	10	pronounced
M ₁	17	10	7	pronounced
M ₂	17	9	10	moderate
M ₃	21	7	14	very slight
<i>Right ramus</i>				
P ₃	18	12	10	pronounced
P ₄	17	12	10	pronounced
M ₁	16	11	—	broken
M ₂	17	9	9	moderate
M ₃	22	7	14	very slight

Explanation of measurements for upper teeth:

AP Taken at base of tooth, greatest distance from anterior part of parastyle to posterior part of metastyle

T Taken at base of tooth, greatest distance from lateral part of mesostyle to center of lingual margin

C Taken parallel to lateral ribs, height of crown from enamel-dentine border to metacone at occlusal surface.

Explanation of measurements for lower teeth:

AP Taken at base of crown, greatest distance from anterior part of paraconid to posterior part of entoconid

T Taken at base of crown, perpendicular to lingual margin, widest distance across talonid

C Taken perpendicular to occlusal surface, height of crown from enamel-dentine border to metaconid-metastylid complex at occlusal surface.

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Genus *Merychippus* Leidy, 1857

Merychippus, species indeterminate

Plate VII E, G

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Hemingfordian to Clarendonian of North America.

Referred specimens.—KUPV 40359a, fragment of upper cheektooth. KUPV 40359b, mandible with P₄, M₁, M₃. KUPV 40359c, isolated lower cheektooth. UWBM 62814, unworn P₂ (?).

Measurements (in mm).—KUPV 40359a, AP = 19. KUPV 40359b: P₄, AP = 20, T = 16; M₁, AP = 18, T = 16; M₃, AP = 25, T = 12; tooth row from anterior M₁ to posterior M₃ = 81. KUPV 40359c, AP = 21, T = 17. UWBM 62814, AP = 22, T = 9.

Description and comparison.—All but KUPV 40359c (Pl. VII E, G) are at stages of wear that make meaningful comparisons impossible. KUPV 40359c cannot be differentiated from comparably worn *M. republicanus* (Niobrara River Fauna), or *M. californicus* (Coalinga). The occlusal pattern of KUPV

40359c bears closest resemblance to that in *M. republicanus*. KUPV 40359c differs from *M. proplacidus* in possessing more prominent roots, from *M. intermontanus* in smaller size and lower crowns, from *M. insignis*, *M. calmaris*, *M. severus* in lacking insertion of the labial V between the metaconid-metastylid complex, from *M. eohipparion* in larger size, from *M. carrizoensis* and *M. primus* in possessing a narrower labial V that does not insert between the metaconid-metastylid complex, from *M. gunteri* in higher crowns and larger size, and from *M. brevidontus* in higher crowns.

Discussion.—These horse teeth fall well within the range of variation exhibited by Barstovian and Clarendonian species of *Merychippus*.

Genus *Parahippus* Leidy, 1858

Parahippus tyleri Loomis, 1908

Plate VII D, F, H, I

Merychippus sp. Sutton and Black (1972), in part.

Merychippus sp. Love, McKenna and Dawson (1976), in part.

Parahippus tyleri Sutton and Black (1972), in part.

Parahippus tyleri Love, McKenna and Dawson (1976), in part.

Locality.—East Pilgrim 5, UWBM loc. C0240.

Age.—Early Hemingfordian.

Range of species.—Early Hemingfordian Runningwater Formation, Nebraska (questionable type locality, Sutton and Black, 1972).

Referred specimens.—CMNH 21617a, 2 upper cheek teeth. CMNH 21617b, left and right mandible with P₃–M₃.

Measurements.—Table 14.

Description and comparison.—Upper teeth from Jackson Hole, like fossils of *P. tyleri* from the Runningwater Formation (F:AM 173-1480, 385-2414, 200-2473, 109856) are distinct from teeth of most other species of *Parahippus* in large size, high crowns, and the presence of cement (Pl. VII H, I). CMNH 21617a and Runningwater specimens of *P. tyleri* differ from teeth of *P. avus* in having a less bulbous protocone, smaller hypostyle, and one or two less plications on the metaloph. CMNH 21617a resembles a specimen from Chalk Cliffs (McKenna, 1955) in simple plications, but is higher crowned with a less bulbous protocone.

The lower teeth (Pl. VII D, F) have the typically rounded labial margins of *Parahippus tyleri* like referred specimens from the Runningwater Formation (F:AM 109856, 393-2787). A prominent external cingulum is present. On M₃ cement partially fills the interstices between the protoconid and hypoconid,

the hypoconid and hypoconulid, and the metastylid and entoconid. As in the upper dentition, the crowns are relatively high in specimens from Jackson Hole and *P. tyleri* from the Runningwater Formation. The two nearly unworn M_3 's measure 14 mm from the enamel-dentine border at the base of the crown to the top of the metaconid. The high crowns, large size, and presence of cement of M_3 suggest that the upper and lower teeth from Jackson Hole are from the same species.

Discussion.—The type locality for *P. tyleri* is not known, but is probably within the Runningwater Formation (Sutton and Black, 1972, from communication by M. F. Skinner). Several referred specimens of *P. tyleri* (F:AM 173-1480, 385-2414, 200-2473, 109856, 393-2787) have been found in the Runningwater Formation.

Order Artiodactyla Owen, 1848

Family Merycoidodontidae Thorpe, 1923

Subfamily Merychyinae Simpson, 1945

Genus *Merychius* Leidy, 1858

Merychius arenarum Cope, 1884

Plate VIII A

Locality.—East Pilgrim 11, UWBM loc. C0239.

Age.—Late Arikareean.

Range of species.—Late Arikareean of Nebraska and Wyoming (Marsland Formation), and Lemhi Valley of Idaho (Table 15).

Referred specimen.—UWBM 63621, fragments of skull with M^2 – M^3 , humerus, 2 distal radii and ulnae, vertebra, probably from single individual.

Description and comparison.—UWBM 63621 is larger than specimens of *M. minimus*, *M. calaminthus*, *M. jahnsi*, and *M. crabilli*, evidenced by orbital diameter (measurement A, Pl. VIII) and length of M^3 (Table 15). In UWBM 63621, the orbit is nearly square and the zygomatic arch is laterally compressed, unlike the rounder orbits and flared zygomatic arches of *M. elegans*, *M. siouxensis*, and *M. (Metoreodon)*. UWBM 63621 further differs from *M. (Metoreodon)* in the deeper zygomatic arch (Pl. VIII A, Table 15, ratio B/A). In *M. siouxensis* and *M. verrucomalus*, the arch is even deeper; the arch in *M. verrucomalus* also differs in having a distinct tuberosity (Stevens, 1970). The Jackson Hole specimen cannot be distinguished from *M. arenarum*. The orbital region of UWBM 63621 closely resembles that in skulls of *M. arenarum* from the Lemhi Valley, Idaho (AMNH 44827, 44829, 44830), from the type area at Platte County, Wyoming (AMNH

8145, 8149, F:AM 33374, 34403, 44583), and from Goshen County, Wyoming (F:AM 44598, 43288, 43270, 44533A).

Merychius, species indeterminate

M. arenarum Colbert (1943).

M. sp. Schultz and Falkenbach (1947).

M. sp. Love (1956).

M. arenarum Black (1968).

M. sp. Sutton and Black (1972).

M. elegans Love, McKenna, and Dawson (1976).

Localities.—Northwest bank of East Pilgrim Creek between outcrops 11b and 5 (Saunders locality).

Age.—Hemingfordian?

Range of genus.—Arikareean to early Barstovian of Nebraska, Wyoming, Idaho, South Dakota, California, Colorado, Table 15.

Referred specimens.—AUG-V120, rostrum and mandible with complete dentition. (This specimen has recently been located at the AMNH, where it is now housed as AMNH 89677.)

Description and comparison.—AUG-V120 was not available for inspection. Descriptions and illustrations by Colbert (1943) and Schultz and Falkenbach (1947) suggest that the specimen is larger than skulls of *M. minimus*, *M. verrucomalus*, and all Arikareean species of *Merychius* except *M. siouxensis*. AUG-V120 differs from *M. siouxensis* in its smaller upper canines, shorter dental series from P^1 to M^3 , and more convex rostrum between the incisors and nasals. Unlike M^1 in *M. arenarum*, that in AUG-V120 is relatively short (Colbert, 1943). Schultz and Falkenbach felt that AUG-V120 differed from species of *M. (Metoreodon)* in lacking “suggested cusps” on P_2 – P_4 . More detailed descriptions of these differences were not given. AUG-V120 most closely resembles skulls of *M. elegans* in dimensions and dental morphology, but is slightly narrower (Schultz and Falkenbach, 1947).

Discussion.—The exact geographic position of AUG-V120 is unknown, but must lie stratigraphically between Units 5 and 28. The original locality description places the fossil, which was found *in situ*, “in an eroding slope on the northwest bank of the south [=east] fork of Pilgrim Creek, one mile above the juncture of this fork with the north fork” (Colbert, 1943:298). Outcrops 5, 8, 8B, and 11B fit this description best (Fig. 2). Outcrop 5 is the most productive Miocene site along East Pilgrim Creek. Scraps of bone occur at outcrop 8. Beds in outcrop 11B correlate with Unit 5, which yielded a skull of *Merychius arenarum* (UWBM 63621) from nearby outcrop 11.

Table 15.—Comparison of characters in specimens of *Merychys*. See explanation.

Age and region	Specimen	Characteristic						
		Size of orbit (A)	Depth of zygoma (B)	B/A	Shape of orbit	Ven-tral zygoma	Humerus LEN/WID	M ¹ AP/T
Jackson Hole Species								
Wyoming	UWBM 63621	29	23	0.79	S	ZCS	92 mn/20	22/16
	AUG V-120	—	15	—	—	—	—	19/—
Late Hemingfordian and Early Barstovian (See Note 1 in explanation)		<i>Merychys (Metoreodon) relictus</i>						
Nebraska	F:AM 33635	—	21	—	—	—	—/22	—
	F:AM 43078	22	14	0.64	CRA	ZF	—	20/16
	F:AM 34319*	26	14	0.53	CRA	ZF	—	21/16
Early Hemingfordian (See Note 2 in explanation)		<i>Merychys elegans</i>						
Nebraska	UNSM 7-10-9-38	26	17	0.65	E-R	ZFR	—	22/16
	UNSM 3-5-8-36	26	22	0.84	E-R	ZFR	—	20/16
		<i>Merychys verrucomalus</i>						
	See Stevens, 1970	24	21–31	0.91	R	T	—/26	18.5–22.1 14.6–16.1
Late Arikareean (see Note 3 in explanation)		<i>Merychys arenarum</i>						
	AMNH 8146*	30	19	0.63	RP	ZF	—	19/16
	Range	21–31	11–25	0.44–0.95	—	—	—	16–24/12–18
Nebraska, Wyoming, Idaho	Mean	26.2	18.3	0.67	—	—	—	20.09/15.34
	Std. dev.	2.42	2.89	0.44	—	—	—	1.78/1.83
	No. specimens	45	46	44	—	—	—	41/38
	F:AM 43277	—	—	—	—	—	130/24	—
	F:AM 43279	—	—	—	—	—	120/28	—
	F:AM 44827	—	—	—	—	—	110/26	—
		<i>Merychys minimus</i>						
Nebraska, Wyoming, South Dakota	CMNH 1466*	22	16	0.72	R	ZCS	—	20/14
	F:AM 33364	20	18	0.90	S	ZCS	—/20	18/14
	F:AM 44610	—	—	—	—	—	—/16	—
Arikareean (See Note 4 in explanation)		<i>Merychys calaminthus</i>						
	LACM 1383	—	—	—	—	—	—	15.5/11.8
		<i>Merychys jahnsi</i>						
California	LACM 1382	—	—	—	—	—	—	13.6/12.0
		<i>Merychys crabilli</i>						
	UNSM 1-1-7-33*	—	15	—	—	—	—	—
	F:AM 45384A	24	14	0.58	S	ZF	—	18/14
	F:AM 4538Z4	—	—	—	—	—	100/23	—
	F:AM 45384Z5	—	—	—	—	—	90/22	—
	Range in 10 specimens from type locality (Schultz and Falkenbach, 1947:Chart 3)							15.2–18.0 11.7–13.7
		<i>Merychys siouxensis</i>						
Nebraska	AMNH 13774	22	19	0.86	R	ZF	—	22/18

See Plate VIII for explanation of measurements. Except for the Jackson Hole specimens, *M. arenarum* skulls and teeth, and *M. verrucomalus*, measurements are from tables and illustrations in Schultz and Falkenbach (1947).

Abbreviations:

- S = square.
 mn = minimum.
 E-R = elongate anteroposteriorly and round.
 R-P = round posteriorly.
 ZCS = zygomatic arch laterally compressed and slender in ventral view.
 ZFR = zygomatic arch laterally flared and robust in ventral view.
 ZF = zygomatic arch laterally flared in ventral view.
 CRA = orbit compressed anteroposteriorly and round.

Table 16.—Stratigraphic occurrence of species of *Merycochoerus*.

Age	Species and formation	Location
Early Hemingfordian	<i>Merycochoerus proprius proprius</i> Runningwater Formation ¹	Nebraska
	<i>Merycochoerus proprius magnus</i> Runningwater Formation? ²	Nebraska
	Arikaree Formation ³	Colorado (Martin Canyon)
Late Arikareean	<i>Merycochoerus matthewi</i> Marsland Formation ⁴	Nebraska and Wyoming
	Rosebud Formation ^{5,6}	South Dakota

¹ Schultz and Falkenbach, 1940 (=Upper part of Marsland Formation).

² Schultz and Falkenbach, 1940 (Stratigraphic position uncertain, but not found with *M. matthewi*, which is confined to the "lower part of the Marsland Formation [p. 289]; intermediate in evolutionary stage between *M. matthewi* and *M. proprius proprius*).

³ Galbreath, 1953 (= "Pawnee Creek Formation").

⁴ Schultz and Falkenbach, 1940 (=Lower part of Marsland Formation).

⁵ MacDonald, 1963.

⁶ MacDonald, 1970.

Subfamily Merycochoerinae Schultz and
Falkenbach, 1940

Genus *Merycochoerus* Leidy, 1858

Merycochoerus proprius magnus (Loomis, 1924)
Plate VIII B

Merycochoerus? Love (1956), in part.

Merycochoerus? Black (1968), in part.

Merycochoerus? Sutton and Black (1972), in part.

Ticholeptus Love (1956).

Brachycrus Love, McKenna, and Dawson (1976), in part.

Locality.—East Pilgrim 5, UWBM loc. C0240.

Age.—Early Hemingfordian.

Range of genus.—Table 16.

Referred specimen.—USNM 17919, in part. Rostrum and anterior mandible, vertebrae, fragments of humerus, radius, ulna, pelvis, femur, tibia, fibula, metapodials, podials.

Description and comparison.—Unlike the condition in *Ticholeptus*, *Merychyus*, and *Ustatochoerus*, the infraorbital foramen is located above M¹ in USNM 17919 (Pl. VIII B). *Merychyus* further differs in being more hypsodont. In lateral view, *Ticholeptus* shows a more gentle slope and straighter dorsal profile of the maxilla and premaxilla between the incisors and nares. In contrast, the lateral profile of the rostrum in USNM 17919 curves convexly between incisors and nasal vacuity, forms a flat platform in the vicinity of the nares, then curves sharply dorsad (Pl. VIII B). In these respects, it resembles *Mediochoerus* and *Merycochoerus*. *Brachycrus* dif-

fers in possessing a facial cavity and infraorbital foramen above M². All of these characters are illustrated by Schultz and Falkenbach (1940, 1941, 1947).

In proportions of the rostrum (ratios NV/PM, DEPTH2/DEPTH1, DEPTH2/C-M), USNM 17919 more closely resembles *Merycochoerus* than *Mediochoerus* (Table 17). The relatively long premaxillary suture ending in a dorsal protrusion (PR, Pl. VIII B) is particularly characteristic of *Merycochoerus proprius proprius* and *M. proprius magnus*. The rostrum in the Jackson Hole specimen begins to increase in depth between P⁴ and M¹. In this respect it resembles *Mediochoerus blicki* and a referred specimen of *Merycochoerus proprius magnus* (F:AM 37520). The depth increase begins slightly more posterior, that is, over M¹, in the type of *Merycochoerus proprius magnus*, over posterior M¹ or anterior M² in *M. proprius proprius*, and over P³ in *M. matthewi*.

The occluded dentition in the Jackson Hole specimen prevents detailed description. The upper canine is about the same size as the incisor, differing from the relatively large canines of *M. proprius proprius*, *M. proprius magnus*, and *M. matthewi*. A 5 mm diastema separates P¹ from the canine and P². P¹, composed of a single oblique blade, is the largest antemolar and P² possesses a small posterior shelf. Other premolars and the incisor are broken. The molars are relatively brachyodont, with the distance from the enamel-dentine border to the tip of the

Note 1.—*M. (Metoreodon) relictus* was found in the "Lower Snake Creek" of Schultz and Falkenbach (1947), which probably equates with the early Barstovian Olcott Formation of Skinner et al. (1977). *M. (M.) relictus taylori* occurs in the late Hemingfordian Sheep Creek Formation of Skinner et al. (1977).

Note 2.—Type of *M. elegans* found in "upper Marsland Fm." of Schultz and Falkenbach (1947) (=Runningwater Formation of McKenna, 1965). Referred specimens with locality data from Dunlap Camel Quarry NE of Hemingford, Sand Canyon Quarry (Sand Canyon locality), Potter Quarry (Sand Canyon drainage system), Hemingford Quarry 2, 7B, 11B, 12A, 12C, 12D, 17, 21, 23 (all Nebraska), and Martin Canyon, Colorado.

Note 3.—Cited as "Lower Marsland" by Schultz and Falkenbach (1947), here considered correlative to the "Upper Harrison beds" of Hunt (1985).

Note 4.—Cited as "Harrison equivalent" by Schultz and Falkenbach (1947).

Table 17.—Measurements of *Merycochoerus* and *Mediochoerus*.

Specimen and statistics	Measurement*													
	PM	NV	NV PM	DEPTH1	DEPTH2	C-M	DEPTH1 DEPTH1	DEPTH2 DEPTH2	C-M C-M	MND	ROSLN	M ¹	M ²	HUM WID
USNM 17919	53	26	0.49	55	44	49	0.80	0.89	34	64	18	26a	51	121
F:AM 42469 ¹	108	38	0.35	118	70	73	0.59	0.96	54	124	22	32	60-66	124-136
Mean, N = 7	91.4	34.6	0.39	109.6	70.3	—	0.66	—	—	—	—	—	—	—
Std. dev.	21.1	6.2	0.10	24.0	10.3	—	0.10	—	—	—	—	—	—	—
AMNH 14242 ¹	69	48	0.70	86	58	76	0.67	0.76	60	104	20	26	64	172
F:AM 37520	76	32	0.42	79	50	—	0.63	—	—	—	—	—	—	—
AMNH 12970 ¹	30	42	1.40	70	38	64	0.54	0.59	40	72	19	26	—	—
Mean, N = 6	36.1	48	1.34	78.3	42.8	—	0.57	—	—	—	—	—	—	—
Std. dev.	4.7	4.9	0.17	19.8	4.4	—	0.13	—	—	—	—	—	—	—
F:AM 43172	33	40	1.21	55	32	47	0.58	0.68	—	52	18	24	—	—
F:AM 43173	35	29	0.83	—	36	—	—	—	—	—	—	—	—	—
USNM 2-11-8-36 ²	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 24439	17	28	1.65	66	27	0.41	—	—	—	—	13	18	—	—

¹ Measurements from Schultz and Falkenbach, 1940.
² Measurements from Schultz and Falkenbach, 1941.
 * Measurements with the following exceptions: DEPTH1, HUM WID, greatest width across distal portion of humerus, TIB LEN, greatest length along lateral edge of tibia.
 a = at least.

Table 18.—Measurements of *Desmatochoerus leidy*.

Measurement*	AMNH 89724	Other specimens†
Basal length of skull	295 mx	280–285
Maximum width of skull	176	—
P ¹ –M ³	145 mx	131–139
P ₁ –M ₃	153 mx	148
M ₃ AP	43 mx	38–39

* See Schultz and Falkenbach (1968:472) for definition of measurements.

† Measurements from Schultz and Falkenbach (1954).
mx maximum.

nearly unworn metacone on M² measuring 23 mm. The mesostyles are moderately developed.

The lower canines are nearly twice the size of the incisors, relatively larger than in *M. matthewi* but resembling other species of *Merycochoerus*. P¹ is nearly as large as the canine. Other teeth are either broken or too tightly occluded for safe separation. Epiphyses are not fused on the postcranial bones, indicating that the individual was young.

Discussion.—The long premaxillary suture, combined with an increase in rostrum depth between P⁴ and M¹, cause referral to *M. proprius magnus*. Individual variation and young ontogenetic age easily account for the small canines and small size of the Jackson Hole specimen, especially in view of the variation known to occur within species of *Merycochoerus* (Schultz and Falkenbach, 1940:278).

The postcranial material here referred to this small individual of *Merycochoerus* may have been attributed to *Brachycrus* by previous workers (Love, 1956; Black, 1968; Sutton and Black, 1972). I refer it to *Merycochoerus* based on its close association with the skull, although postcranial morphology of *Brachycrus* and small specimens of *Merycochoerus* has not been shown to be diagnostic. In examining all of the oreodonts collected by Love in 1945, I found no other bones that could logically be attributed to *Brachycrus*.

Merycoidodontidae, species indeterminate

Merycochoerus? Love (1956), in part.

Merycochoerus? Black (1968), in part.

Merycochoerus? Sutton and Black (1972), in part.

Merycochoerus Love, McKenna, and Dawson (1976), in part.

Locality.—East Pilgrim 5, UWBM loc. C0240.

Age.—Early Hemingfordian.

Referred specimens.—USNM 17919, in part. Sacrum, 2 femora, 2 tibiae, articulated tarsals and metatarsals, probably from same individual.

Measurements (in mm).—Lateral length of 2 femora, 245, ±245. Lateral length of 2 tibiae, 151, 147.

Discussion.—The bones represent a large oreodont that approaches *Megoreodon*, *Desmatochoerus*, *Promerycochoerus*, *Merycochoerus*, or *Usta-tochoerus* in size. These bones were recovered in association with those of the small *Merycochoerus proprius magnus* that is described above (J. D. Love, personal communication, 1980), but obviously represent a significantly larger individual.

Subfamily Desmatochoerinae Schultz and Falkenbach, 1954

Genus *Desmatochoerus* Thorpe, 1921

Desmatochoerus leidy (Bettany, 1876)

Plate IX

Promerycochoerus leidy Love, McKenna, and Dawson (1976).

Locality.—Emerald Lake SR, UWBM loc. C0241.

Age.—Late Arikareean.

Range of species.—Arikareean: John Day Formation of north-east Oregon (Bridge Creek, the Cove, Butler Basin) (Schultz and Falkenbach, 1954).

Referred specimens.—AMNH 89724, skull and mandible with dentition. Questionably referred, UWBM 63262, anterior portion of rostrum that may belong to same individual as AMNH 89724.

Description and comparison.—AMNH 89724 is referred to *Desmatochoerus* rather than *Promerycochoerus* on the basis of relatively narrow skull (less than 190 mm) (Table 18), narrow braincase, thin sagittal crest, small laterally compressed bullae, very robust dentition, robust styles, and laterally compressed paraoccipital processes. All species of *Promerycochoerus*, in contrast, show wide skulls (190–322 mm), inflated braincase, robust sagittal crest, large bullae, moderately heavy dentition, small styles, and laterally compressed paraoccipital processes (Schultz and Falkenbach, 1949, 1954).

AMNH 89724 cannot be differentiated from *Desmatochoerus leidy* except for slightly larger size (Table 18). All measurements that indicate larger size, however, are maximum estimates because the premaxilla and posterior portions of the third molars are missing or distorted. Other species of *Desmatochoerus* are definitely smaller, with basal length not exceeding 270 mm (Schultz and Falkenbach, 1954:160).

Family Camelidae Gray, 1821

Genus *Aepycamelus* MacDonald, 1956

Aepycamelus, species indeterminate

Locality.—Two Ocean Lake, UWBM loc. C0238.

Age.—Late Barstovian.

Range of genus.—Hemingfordian to Clarendonian (Wood et al., 1941).

Referred specimen.—UWBM 63267, portions of partially articulated vertebrae, humerus, radioulna, metacarpal, tibia, astragalus, phalanges of single individual.

Measurements (in mm).—Astragalus: Width, 43. Lateral length, 67. Medial length, 61.

Medial phalanx: Length, 90, Proximal width, 33. Distal width, 24.

Tibia: Distal width, 69.

Radius: Length, 510. Proximal width, 64. Transverse diameter at center of shaft, 48. Distal width, 62.

Composite radioulna: Length, approximately 593.

Metacarpal (?): Length, minimum 400 (broken). Transverse diameter, ± 50 .

Humerus: Distal width, 63.

Longest cervical vertebra (broken): Minimum length, 160. Narrowest diameter of centrum, 33.

Discussion.—The large size, long cervical vertebrae, and elongate, slender limb bones suggest the genus is *Aepycamelus*.

Genus *Oxydactylus* Peterson, 1904

?*Oxydactylus*, species indeterminate

Locality.—East Pilgrim Creek between outcrops 11b and 5 (Saunders locality).

Age.—Hemingfordian.

Range of genus.—Arikareean, Hemingfordian (MacDonald, 1963, 1970).

Referred specimens.—AUG-V121, podials and fragmentary metapodial. (These specimens are now at the AMNH, catalogued as AMNH 101148.)

Discussion.—I have not examined this material and rely on the identification by Colbert (1943), who illustrated the specimens.

Family Antilocapridae Gray, 1866

Genus *Merycodus* Leidy, 1854

Merycodus, species indeterminate

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Hemingfordian to Clarendonian (Wood et al., 1941).

Referred Specimen.—KUVP 17482, mandible fragment with worn M_2 – M_3 .

Measurements (in mm).— M_2 : AP = 9, T = 6. M_3 : AP = 1.3, T = 6.

RESULTS

At least 32 species of Miocene mammals occur in the Colter Formation and represent faunas of three distinct ages—Arikareean, Hemingfordian, and Barstovian. Faunal groups from different parts of the Colter are designated here as the Emerald Lake Fauna (late–early Arikareean age), the East Pilgrim Assemblage (includes three sparsely represented local faunas that range from the late Arikareean to the early Hemingfordian), and the Cunningham Hill Fauna (late Barstovian age).

FAUNAL AGES

Emerald Lake Fauna (late–early Arikareean)

The Emerald Lake Fauna consists of the species recovered from Unit 1 at Emerald Lake SR (UWBM loc. C0241) (Table 19). Except for a single oreodont rostrum, all of the fossils from the very limited exposure were reported by Love et al. (1976), and McKenna kindly made them available to me for examination. *Allomys cristabrevis*, new species, which is slightly more primitive than *Allomys harkseni* from the Monroe Creek Formation and decidedly more primitive than all but the oldest species from the John Day Formation (*A. cavatus*, Rens-

berger, 1983), implies correlation with about the middle of the *Meniscomys* Concurrent-range zone. Rensberger (1981) concluded that the other apodontid, *Niglarodon* sp., suggests correlation with the top of the *Meniscomys* Concurrent-range Zone. Unit 1SR, therefore, probably falls somewhere within the upper half of this zone. The occurrence of *Desmatochoerus leidy* and *Archaeolagus emeraldensis*, new species, is compatible. The only other reported specimens of *D. leidy* occur within the John Day Formation, but precise locality data are lacking. Based on stage of evolution, Shultz and Falkenbach (1954, 1968) considered species of *Desmatochoerus* to range through strata contemporaneous with the Gering, Monroe Creek, and Harrison Formations. They considered *D. leidy* to have come from strata “approximately equal in age to the Harrison Formation of the central Great Plains” (1954:185). *Archaeolagus emeraldensis*, new species, is morphologically most similar to, but perhaps slightly more advanced than, *A. ennisianus*, which is found in the John Day Formation (Dawson, 1958:42). More precise locality data for *A. ennisianus* are not available. Like *A. ennisianus*, *A. emeraldensis* possesses a longer P_3

Table 19.—Faunal list for Emerald Lake Fauna.

Rodentia
Aplodontidae
<i>Niglarodon</i> sp.
<i>Allomys cristabrevis</i> , new species
Lagomorpha
Leporidae
<i>Archaeolagus emeraldensis</i> , new species
Artiodactyla
Merycoidodontidae
<i>Desmatochoerus leidy</i>

and is smaller than average for late Arikareean *A.* cf. *A. macrocephalus* and early Hemingfordian *A. macrocephalus*. I follow Fisher and Rensberger (1972), Rensberger (personal communication, 1983), and Woodburne and Robinson (1977) in considering the upper half of the *Meniscomys* Concurrent-range Zone, and by inference Unit 1SR at Emerald Lake, to approximately correlate with 23.6 to 24.6 my on the radiometric scale. Radiometric dates of about 26 to 29 my have been determined near the base of the *Meniscomys* Concurrent-range Zone in the John Day and Gering Formations (Fisher and Rensberger, 1972; Evernden et al., 1964; Obradovich et al., 1973; Rose and Rensberger, 1983). The middle of the overlying *Entoptychus-Gregorymys* Concurrent-range Zone was K-Ar dated at 21.9 my in the Harrison Formation (Fisher and Rensberger, 1972; Evernden et al., 1964).

East Pilgrim Assemblage
(late Arikareean to early Hemingfordian)

Fossils from East Pilgrim 11 (UWBM loc. C0239), the Saunders locality, and East Pilgrim 5 (UWBM loc. C0240), comprise the East Pilgrim Assemblage (Table 20). The localities span a considerable stratigraphic distance, Units 5 through 28, but each produced few specimens. They are here artificially grouped into the same assemblage merely for convenience. Each locality is discussed separately, because differences in age are probable.

East Pilgrim 11 local fauna (late Arikareean), from UWBM loc. C0239, Unit 5.—The only specimen from this site, UWBM 63621, is an oreodont skull that cannot be differentiated from skulls of *Merychyus arenarum*. *M. arenarum* is known only from the Marsland Formation *sensu* McKenna (1965) (here considered equivalent to the "Upper Harrison" beds of Hunt, 1985) in the superposed se-

Table 20.—Faunal lists for East Pilgrim Assemblage.

East Pilgrim 5 local fauna (from Unit 28):
Perrisodactyla
Equidae
<i>Parahippus tyleri</i>
Artiodactyla
Merycoidodontidae
<i>Merycochoerus proprius magnus</i>
cf. <i>Merycochoerus</i>
Saunders local fauna (from between Unit 5 and 28):
Artiodactyla
Camelidae
? <i>Oxydactylus</i>
Merycoidodontidae
<i>Merychyus</i> (cf. <i>M. elegans</i>)
East Pilgrim 11 local fauna (from Unit 5):
Artiodactyla
Merycoidodontidae
<i>Merychyus arenarum</i>

quence of the Great Plains, and from the Lemhi Valley of Idaho (Schultz and Falkenbach, 1947). Unit 5, like the Marsland Formation, is therefore considered late Arikareean in age (Hunt, 1985). The late Arikareean seems to correlate with about 19 to 23 my in the Great Plains. Dates on various ashes within the Arikaree Group bracket the major intra-Arikareean faunal change between 25 and 22 my to provide the lower limit (Hunt, 1985:194). For example, a 21.9 my date from near the middle of the Harrison Formation (Evernden et al., 1964) was determined from the Agate Ash approximately 10 m below a late Arikareean fauna. The upper limit—that is, the Arikareean-Hemingfordian boundary—appears younger than 19.2 m.y. as indicated by a fission-track date on the Eagle Crag Ash, which lies below the late Arikareean Niobrara Canyon local fauna (Hunt, 1985:177). Radiometric-age determinations associated with Hemingfordian faunas are consistent with placing the end of the Arikareean near 19 my. A date of 21.6 my was obtained between the late Arikareean Black Butte and early Hemingfordian Logan Mine faunas of the Hector Formation in California (Woodburne et al., 1974). The early Hemingfordian Boron local fauna in California occurs stratigraphically above dates ranging from 18.3 to 20.3 m.y. (Whistler, 1984). The late Hemingfordian Philips Ranch, California, and Split Rock, Wyoming, faunas are associated with K-Ar dates of 17.6 and 17.4 my, respectively (Evernden et al., 1964; Munthe, 1979a). The Philips Ranch fauna is above

the dated rocks, and the Split Rock fauna is from strata above and below the dated sample.

Saunders local fauna (early Hemingfordian?), from *East Pilgrim Creek, somewhere between Units 5 and 28*.—The only biostratigraphically useful fossil, recovered by Roy Saunders in the 1930's, represents a species of *Merychyus* that differs from Arikareean species in larger size, smaller upper canines, or both. The specimen most closely resembles skulls of *Merychyus elegans*, an early Hemingfordian species.

East Pilgrim 5 local fauna (early Hemingfordian), from *UWBM loc. C0240, Unit 28*.—Examination of the only material known from this locality was possible through the courtesy of C. C. Black, M. R. Dawson, and R. J. Emry. *Parahippus tyleri* is represented by two upper cheek teeth (CMNH 21617a) and two mandibles with cheek teeth (CMNH 21617b). The upper teeth were previously referred to *Merychippus*, but are morphologically quite similar to other specimens of *P. tyleri* (for example, F: AM 173-1480, 385-2414, 200-2473, 109856), particularly in high crowns (for *Parahippus*), incomplete union of crochet and protoloph, large size, and very thin layer of cement. Lower teeth resemble those of referred *P. tyleri* (F:AM 109856, 393-2787) in high crowns, rounded labial margins, and cement only on M₃. The comparative specimens mentioned above are from the early Hemingfordian Runningwater Formation; the type of *P. tyleri* probably also comes from the Runningwater (Sutton and Black, 1972).

The species of oreodont found in Unit 28, *Merycochoerus proprius magnus*, occurs in the early Hemingfordian Martin Canyon Quarry A Fauna and, from what little stratigraphic data is available for Nebraska specimens, probably also in the Runningwater Formation (Schultz and Falkenbach, 1940). The horse and the oreodont suggest that the age of Unit 28 equates closest with that of the Runningwater Formation, as was also concluded by Sutton and Black (1972). Unit 28 is therefore considered early Hemingfordian age, which according to correlations discussed above ranges from about 18 to 19 my ago. Contrasting with earlier reports, no objective evidence suggests the presence of *Brachycrus* in the Unit 28 assemblage.

Cunningham Hill Fauna (late Barstovian)

By far the most diverse in Jackson Hole, the Cunningham Hill Fauna includes assemblages from Cunningham Hill (UWBM loc. C0236), North Pilgrim 2 (UWBM loc. C0237), and Two Ocean Lake

(UWBM loc. C0238). Nearly identical faunules characterize the first two localities, and the single fossil from Two Ocean Lake is from a stratigraphic position close to that of Cunningham Hill. Similarities to other faunas that share genera (Fig. 27) imply a late Barstovian age for the Cunningham Hill Fauna. It is no older than Barstovian, based on the occurrence of *Copemys*, *Cupidinimus*, and *Mojavemys*, all of which appear first in the early Barstovian. It is no older than late Barstovian, because *Domninoidea*, *Spermophilus*, *Petauristodon*, *Diprionomys agrarius*, and *Lignimus* are unknown in older faunas. The Cunningham Hill Fauna is probably not younger than late Barstovian because it includes *Oreolagus*, *Monosaulax*, and *Peridiomys*, which are taxa unknown in Clarendonian or younger faunas. *Petauristodon* occurs only in the *Copemys longidens* and the overlying *Copemys russelli* Assemblage Zones of the Barstow Formation (Lindsay, 1972), and *Domninoidea* is present only in the *Copemys russelli* Assemblage Zone. A tuff near the boundary between these zones in the Barstow Formation yielded K-Ar dates of 13.6 to 13.8 my (Lindsay, 1972; Savage, 1977). On the Great Plains, a fission-track date of 11.6 my, or perhaps 13.6 my depending on how the glass standards are calculated, was determined from the Hurlbut Ash between the Niobrara River Fauna and the Norden Bridge Fauna (Skinner and Johnson, 1984:252). The Cunningham Hill Fauna shares with both faunas *Diprionomys agrarius*, *Copemys kelloggae*, and several genera (Fig. 27). It therefore seems likely that the Cunningham Hill Fauna falls between 12 and 14 my on the radiometric scale.

CORRELATIONS

Similarities in small mammals suggest that Unit 1 of the Colter Formation correlates with parts of the John Day, Deep River, and Monroe Creek Formations, Cabbage Patch beds, and with deposits containing the Peterson Creek local fauna (Figs. 28, 29). Large mammals suggest that Unit 5 correlates with the Marsland Formation, and Unit 28 with the Runningwater Formation. Formations that share many faunal elements with Unit O (= ± 69) and Unit 43 include parts of the upper Barstow, the Caliente, and Deer Butte, the Madison Valley, the Valentine, and the Wood Mountain Formations and the Butte Creek Volcanic Sandstone. Most other correlates listed on the charts (Figs. 28, 29) show faunal elements diagnostic of a given age, but do not share elements with the Colter faunas. For the sake of

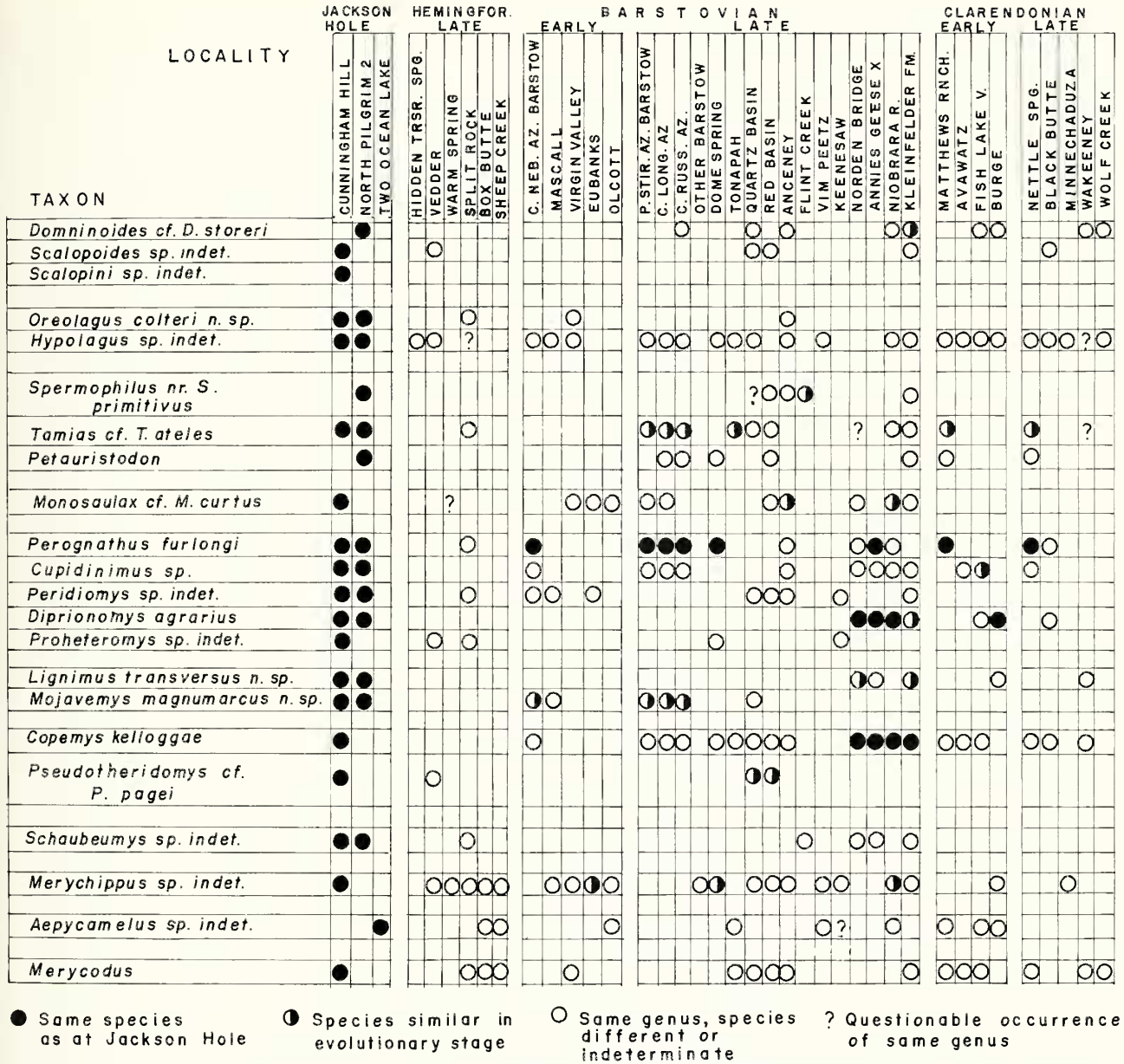


Fig. 27.—Faunal checklist and comparison of the Cunningham Hill Fauna, which includes fossils from North Pilgrim 2 (UWBM loc. C0237), Cunningham Hill (UWBM loc. C0236), and Two Ocean Lake (UWBM loc. C0238).

completeness, the Browns Park, North Park, and Troublesome Formations are included but placed mainly on the basis of radiometric dates. Only published data have been used to construct the charts. Placement of the Barstovian-Clarendonian boundary follows Webb (1969), while correlation of the radiometric chronology with most epochs, provincial ages, and concurrent-range zones agrees with Armentrout (1981) and Woodburne and Robinson (1977). Other sources, as well as dates culled mostly

from Evernden et al. (1964), are listed on the charts. Where appropriate, these authors' correlations have been modified according to the IUGS constants for K-Ar dates set forth by Dalrymple (1979), and to take into account recent dates and stratigraphic work on the Great Plains (Hunt, 1985).

FAUNAL RELATIONSHIPS

At the generic level the Cunningham Hill Fauna resembles late Barstovian faunas from all three geo-

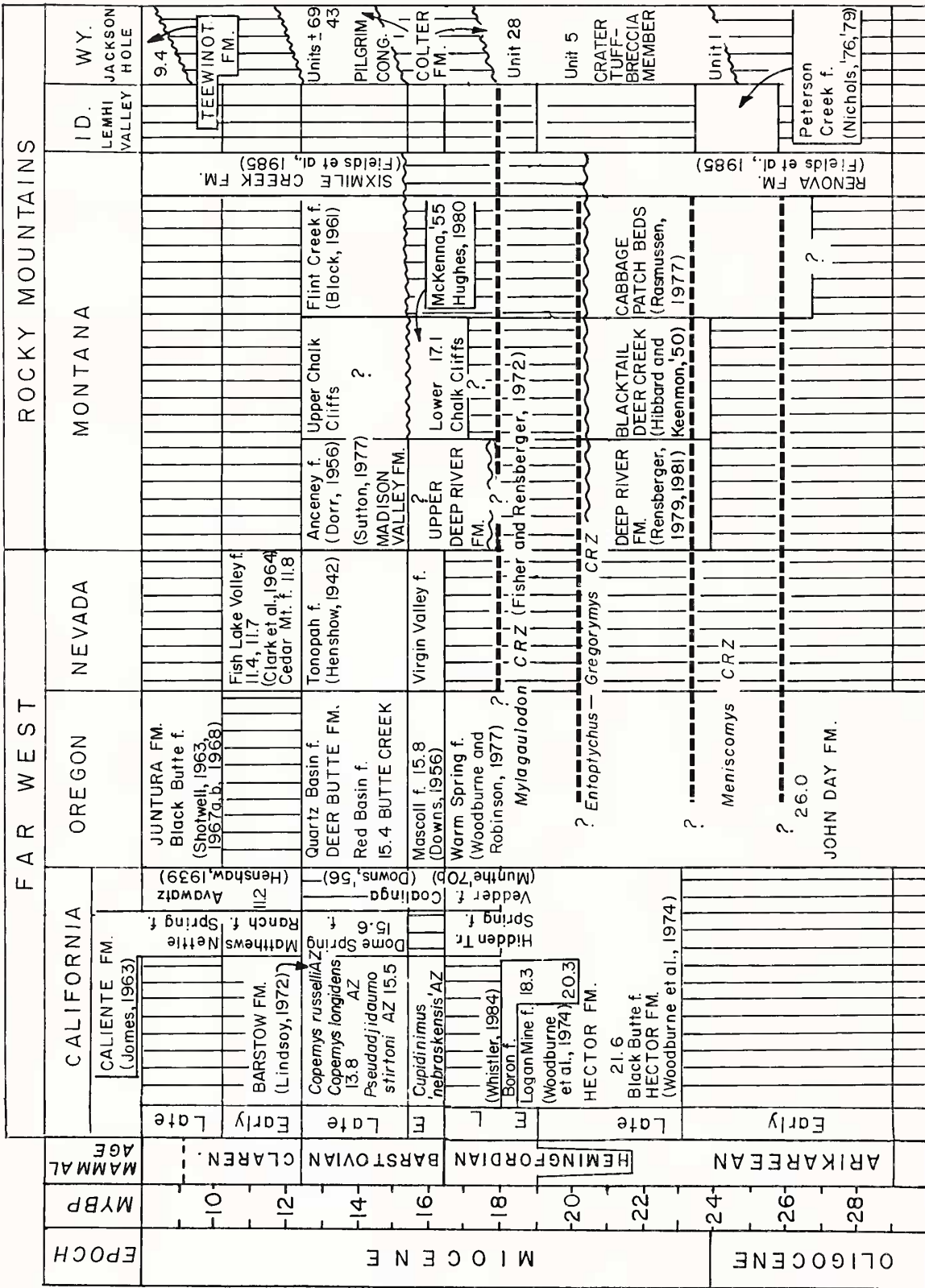


Fig. 28.—Biostratigraphic correlation of the Colter Formation and faunas with rocks (capital letters) and faunas (lower case) of the Far West and Rocky Mountains. Except for the Clarendonian-Hemphillian and the Arkaarean-Hemingfordian boundaries, correlation of the radiometric chronology with epochs and mammal ages is from Armentrout (1981). In Jackson Hole, a K-Ar date of 9.4 my from 32 m below a Hemphillian mammal assemblage (Hibbard, 1970) suggests that the early Hemphillian may be about 1 my older than Armentrout places it. The Arkaarean-Hemingfordian boundary is considered to be at least 2 my younger than Armentrout's assignment on the basis of Hunt's (1985) report of a 19.2 my date from below the typical late Arkaarean Niobrara Canyon local fauna in Nebraska. Placement of concurrent-range zones is modified from Fisher and Rensberger (1972) and Woodburne and Robinson (1977) to conform with movement of the Arkaarean-Hemingfordian boundary, and with Dairymple's (1979) standards for calculation of K-Ar dates. Localities are sorted into the early or late part of provincial land-mammal ages, but closer correlation with the radiometric scale is not intended except where dates are listed.

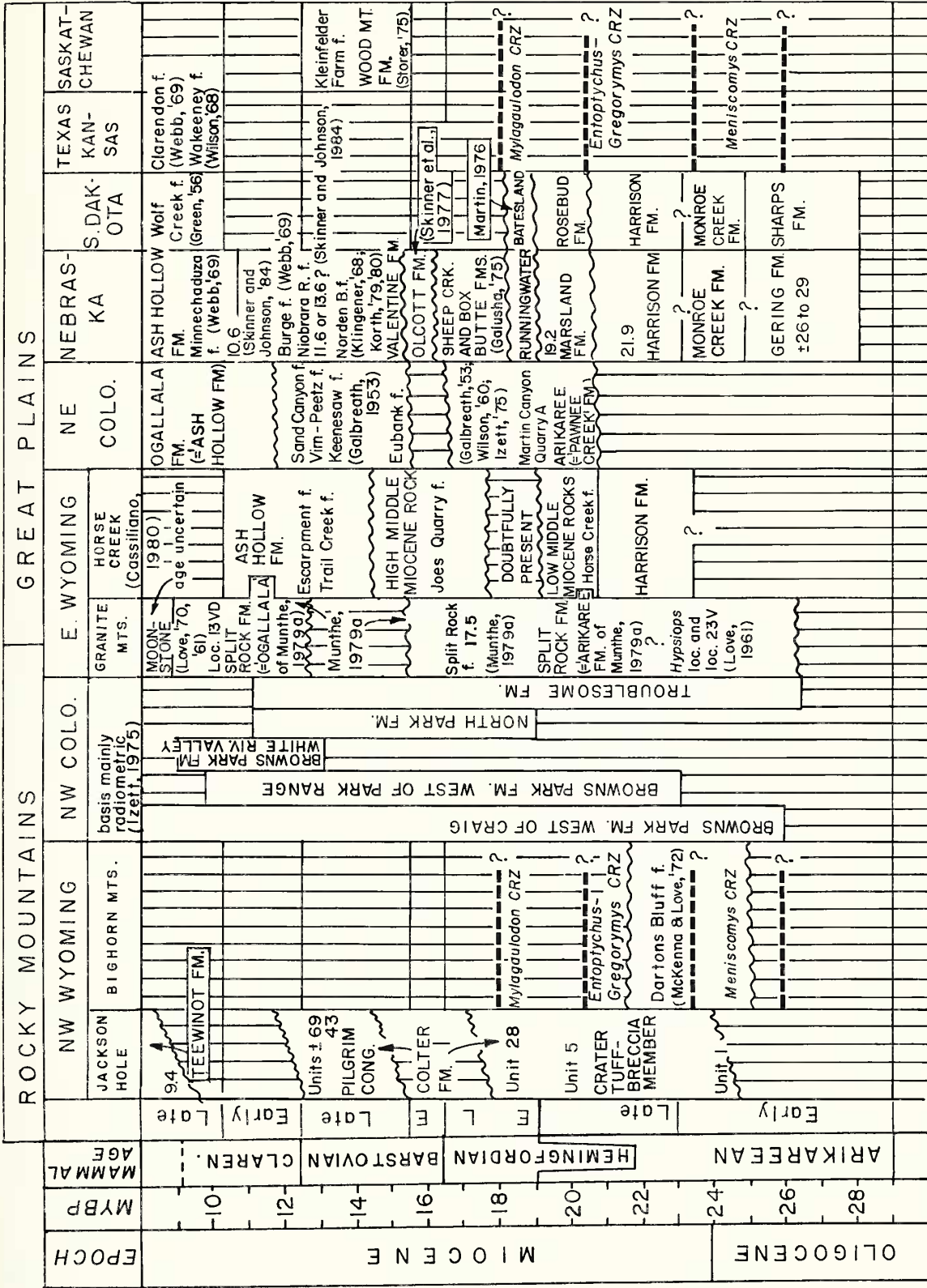


Fig. 29.—Biostratigraphic correlation of the Colter Formation and faunas with rocks and faunas of the Great Plains and Rocky Mountains. See Fig. 28 for further explanation.

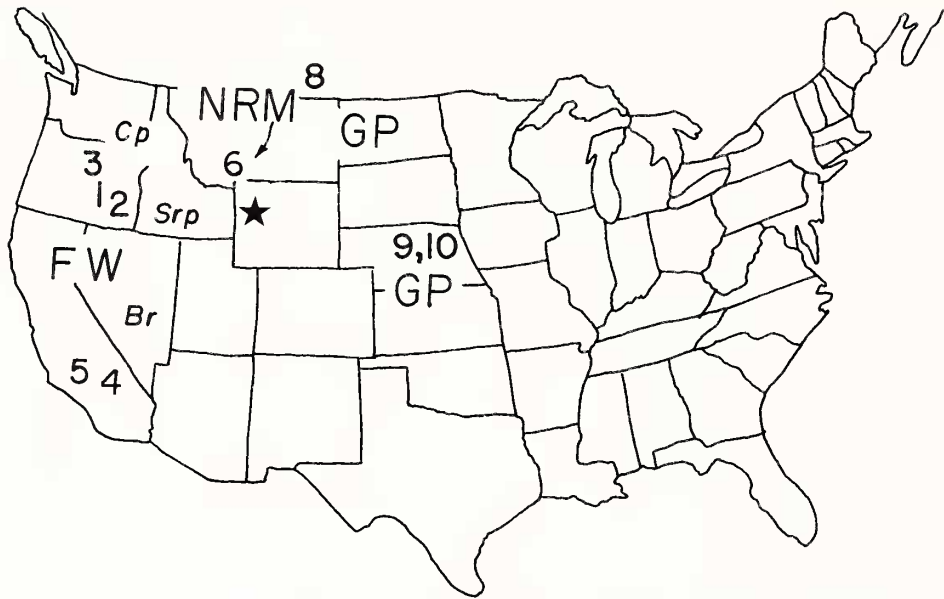


Fig. 30.—Location of Barstovian sites with diverse mammal faunas. Far West (FW): 1, Red Basin (Shotwell, 1968). 2, Quartz Basin (Shotwell, 1968). 3, Mascall (Downs, 1956). 4, Barstow (Lindsay, 1972). 5, Dome Spring (James, 1963). Cp, Columbia Plateau. Srp, Snake River Plain. Br, Basin and Range. Northern Rocky Mountains (NRM): *, Jackson Hole (see Fig. 1 for enlargement). 6, Ancney (Dorr, 1956; Sutton, 1977). Great Plains (GP): 8, Kleinfelder Farm (Storer, 1975). 9, Norden Bridge (Klingener, 1968) and “Niobrara River” (Webb, 1969). 10, Annies Geese Cross Quarry (Korth, 1979, 1980).

graphic regions from which diverse small-mammal assemblages are known—The Far West (including the Columbia Plateau, Snake River Plain, Basin and Range, and West Coast), the Northern Rocky Mountains (mountainous areas of Wyoming and Montana), and the Great Plains (plains east of the Rockies in Colorado, Wyoming, Nebraska, South Dakota, and Saskatchewan) (Fig. 30). At least 11 genera range throughout these geographic regions (Fig. 31). The faunal continuity suggests that genera listed in Fig. 31 can be regarded as characteristic of the late Barstovian. All but *Diprionomys*, *Spermophilus*, and *Scalopoides* are known from the upper member of the Barstow Formation (Lindsay, 1972), strata that Wood et al. (1941) considered to yield faunas typical of Barstovian land-mammal age.

Two genera and three species that occur in Jackson Hole (Fig. 32) are known from the Great Plains but have never been reported from the Far West. One genus and two species, however, show the opposite relationship—they are known from Jackson Hole and the Far West, but not from the Great Plains (Fig. 32). The presence of more Great Plains than western taxa in the Cunningham Hill Fauna may imply greater affinity with eastern faunas, but the differences are not statistically significant. The intermingling of eastern and western taxa at Jackson

Hole, the geographically intermediate site, seems to reflect a gradual west to east change in taxonomic composition of Barstovian faunas. Factors that limited distribution, such as distance, vegetation, physiographic barriers, climate, and competition were apparently affecting individual genera and species rather than entire communities.

The overlap of taxa at Jackson Hole (Fig. 32) leads to the conclusion that the Great Plains faunas that contain *Shaubeomys*, *Diprionomys agrarius*, *Copemys kelloggae*, *Domninoidea storeri*, and low crowned species of *Lignimus* correlate with Far West faunas that lack those taxa but include *Mojavemys*, *Pseudotheridomys pagei*, and *Tamias ateles*. Therefore, faunas at the Norden Bridge and Annies Geese Cross Quarries of the Nebraska Great Plains, considered as “Valentinian” provincial age in the terminology of Schultz et al. (1970, and references therein) probably correlate with the typical late Barstovian faunas of the upper Barstow Formation (Lindsay, 1972). The shared presence of *Cupidinimus*, *Copemys*, and *Perognathus* at these sites is consistent with this hypothesis. The step-wise correlation to the type locality at Barstow suggests that Norden Bridge and Annies Geese Cross quarries are late Barstovian in age. If so, the lower part of the “Valentinian” provincial age overlaps the late Bar-

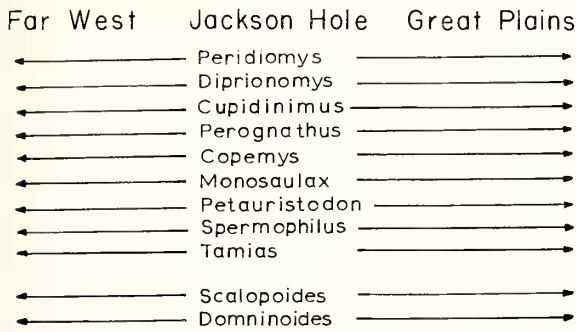


Fig. 31.—Genera that characterize late Barstovian faunas throughout the western United States and southern Saskatchewan.

stovian. Because of this apparent redundancy, the term “Valentinian” is not included on any of the correlation charts.

At least 13 late Barstovian species are found only in Far West faunas, five species are known only from Jackson Hole, and six species are known only from the Great Plains (Table 21). Different ecologic settings in each of the three regions provides the most likely explanation for the three assemblages of species. Wide geographic separation would help to maintain the differences. Distinctive assemblages of Far West, Rocky Mountain, and Great Plains species also characterize modern small-mammal faunas (Hall, 1981). The different modern assemblages coincide with differences in physiography, vegetation, and climate (Trewartha et al., 1968:maps 1, 2, 3, 9). Physiographic differences between the three areas had already developed by the Eocene with uplift of the Rocky Mountains (Love, 1960). During the Hemingfordian and Barstovian, renewed tectonism in the northern Rockies delineated the modern basins and ranges (Rasmussen, 1973; Thompson et al., 1981; Fields et al., 1985). It is, therefore, likely that by the late Barstovian, the Rocky Mountains were prominent highlands that were ecologically separated from the Far West and Great Plains. Ecological separation, as is evident today, would have resulted from differences in vegetation and climate that accompany differences in altitude and distance from oceans.

Paleofloral data provide some independent evidence that the ecologic setting of the Rocky Mountains differed from that of areas to the west and east by Barstovian time. Leopold and MacGinitie (1972: 186) concluded that floras of the Rockies, among them a pollen flora from the lower Colter Formation, were distinct from those of the Far West and eastern U.S. by the middle Eocene. They provided

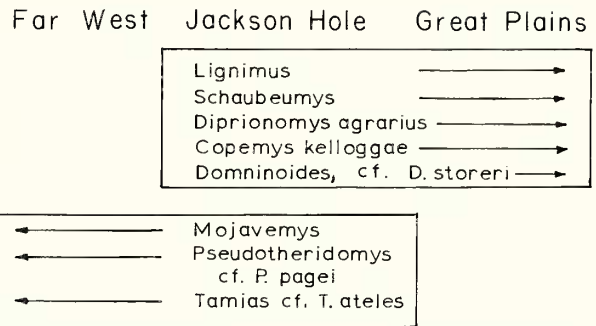


Fig. 32.—Late Barstovian mammals found together at Jackson Hole but usually restricted to either the Far West or Great Plains.

floral lists for the Beaverhead Basin flora (late Oligocene, Montana), Split Rock Formation (Hemingfordian, Wyoming), Trapper Creek flora (mid?-Miocene, Idaho), Moonstone Formation (late Miocene, Wyoming), and Teewinot Formation (Hemphillian, Jackson Hole) that imply coniferous vegetation of continental aspect has grown in the Rockies since the mid-Tertiary. A study of fossil pollen from the Teewinot Formation showed that essentially modern vegetation had arrived in Jackson Hole by the early Hemphillian (C. Barnosky, 1984). In contrast to vegetation of the Rocky Mountains, temperate conifers and broad-leaved deciduous plants were common in Washington, Oregon, Nevada, and northcentral California from at least Arikarean (late Oligocene/early Miocene) to Hemphillian (late Miocene) time (Wolfe, 1969). Vegetation in the Great Plains was more diverse than in the Rockies and related strongly to present Appalachian plants, as evidenced by the late Miocene Kilgore Flora of Nebraska (MacGinitie, 1962; Leopold and MacGinitie, 1972:163).

Table 21.—Species confined to one geographic area.

Far West:	<i>Mojavemys lophatus</i> , <i>Mojavemys mascalensis</i> , <i>Mojavemys alexandrae</i> , <i>Cupidinimus halli</i> , <i>Cupidinimus</i> “ <i>nebraskensis</i> ,” <i>Cupidinimus eurekaensis</i> , <i>Perognathus minutus</i> , <i>Copemys longidens</i> , <i>Copemys esmeraldensis</i> , <i>Copemys russelli</i> , <i>Copemys tenuis</i> , <i>Copemys barstowensis</i> , <i>Copemys dentalis</i>
Jackson Hole:	<i>Lignimus transversus</i> , new species, <i>Mojavemys magnumarcus</i> , new species, <i>Cupidinimus</i> sp., <i>Spermophilus</i> near <i>S. primitivus</i> , <i>Oreolagus colteri</i> , new species
Great Plains:	<i>Lignimus montis</i> , <i>Lignimus</i> cf. <i>L. hibbardi</i> , <i>Cupidinimus nebraskensis</i> , <i>Perognathus trojectionansrum</i> , <i>Copemys niobrariensis</i> , <i>Russellagus vonhofi</i>

Temporal differences between sites of the three geographic regions cannot be discounted, but do not provide the simplest explanation for the geographic restriction of species (Table 21). Related species in the different regions are at a similar evolutionary grade, which would not be expected if morphologic differences were due mainly to temporal isolation. Very low crowned species of *Lignimus* occur at Jackson Hole (*L. transversus*), Kleinfelder Farm (*L. montis*), and Norden Bridge (*L. cf. L. montis*). Low crowned species of *Cupidinimus* are present at Barstow (*C. "nebraskensis"*), Anceney (*C. madisonensis*), Annies Geese Cross Quarry, and Norden Bridge (*C. nebraskensis*). High crowned species of *Mojavemys* with enamel chevrons on upper teeth are present at Jackson Hole (*M. magnumarcus*) and Barstow (*M. lophatus*).

Preservation or collection bias is probably even less important in accounting for the differences between Barstovian species of the three regions (Table 21). The same genera occur in most sites, and the same species are present in some (Figs. 27, 31, 32). Collection bias probably does influence the number of species known to be restricted to one geographic region. The region with the most sites, the Far West,

also has the greatest number of restricted species, 13. That with the fewest sites, Jackson Hole, also has the fewest restricted species, 5.

The few fossils from the East Pilgrim and Emerald Lake faunas prevent any detailed statements about their affinities, but some facts are suggestive. *Merycochoerus proprius magnus* and *Parahippus tyleri* are otherwise known only from Nebraska (both) and northeast Colorado (*M. proprius magnus*). *Merychyus arenarum* is known mainly from Nebraska and eastern Wyoming. Presence of these taxa in the East Pilgrim Fauna implies at least some faunal continuity between Jackson Hole and the Great Plains during the early Hemingfordian.

In the Emerald Lake Fauna three of the four species are new, which is consistent with a postulate of distinct ecologic settings in the Rocky Mountains as far back as the Arikareean. One genus, *Niglarodon*, is known only from the Rocky Mountains and possibly the Great Plains (Rensberger, 1981). *Allomys cristabrevis* is closely related to a Great Plains alomyine rodent, *A. harkseni*. *A. cristabrevis* and *Niglarodon* sp. suggest faunal affinity with the Great Plains. *Desmatochoerus leidyi* provides the only evidence for an overlapping range of a western taxon.

CONCLUSIONS

1. Thirty-two species of mammals are now known from the Colter Formation.

2. Three distinct faunal assemblages are recognized. They are designated the Emerald Lake Fauna, the East Pilgrim Assemblage, and the Cunningham Hill Fauna.

3. The Emerald Lake Fauna most resembles those of the upper half of the *Meniscomys* Concurrent-range Zone (late-early Arikareean).

4. The East Pilgrim Assemblage includes three stratigraphically separated local faunas. The uppermost one, the Unit 28 local fauna, yields species that also are present in the Runningwater Formation (early Hemingfordian). However, the stratigraphically lowest, the Unit 5 local fauna, is represented only by *Merychyus arenarum*, an oreodont that is known otherwise only from the Marsland Formation and rocks equivalent in age to the Marsland (late Arikareean).

5. The Cunningham Hill Fauna is late Barstovian in age and contains taxa that occur only in the *Copemys longidens* and *Copemys russelli* Assemblage zones of the Barstow Formation.

6. Faunal similarities suggest that the oldest bed in the Colter Formation (Unit 1SR) correlates with parts of the John Day (Oregon), Deep River (Montana), and Monroe Creek (South Dakota) Formations, the Cabbage Patch beds (Montana), and with deposits containing the Peterson Creek fauna (Idaho).

7. Tuff near the top of the Crater Tuff-breccia Member (Unit 28) correlates most closely with the Runningwater Formation (Nebraska) because *Parahippus tyleri* and *Merycochoerus proprius magnus* are present.

8. On the basis of directly comparable faunas, the Pilgrim Conglomerate Member (Units 43 and O) correlates with parts of the Barstow (California), Caliente (California), Deer Butte (Oregon), Madison Valley (Montana), and Wood Mountain (Saskatchewan) Formations and the Butte Creek Volcanic Sandstone (Oregon).

9. The Emerald Lake Fauna (Unit 1SR) is about 23.6 to 24.6 my old, the East Pilgrim Assemblage (Units 5 to 28) between 18 and 20 my old, and the Cunningham Hill Fauna (Units 0 to 43) about 12

to 14 my old, based on correlations of the faunal ages with the radiometric scale.

10. *Lignimus*, *Schaubeumys*, *Diprionomys agrarius*, *Copemys kelloggae*, *Domninoidea* cf. *D. storeri*, *Mojavemys*, *Pseudotheridomys* cf. *P. pagei*, and *Tamias* cf. *T. ateles* occur contemporaneously in Jackson Hole. The last three are otherwise reported only from the Far West, and the rest only from the Great Plains.

11. The association mentioned above helps to establish a step-wise correlation that suggests early "Valentinian" and late Barstovian refer to overlapping intervals of time.

12. The late Barstovian and Arikareean faunas in Jackson Hole contain suites of species that differ from those of late Barstovian and Arikareean faunas of the Far West and Great Plains. The differences in species are mainly attributed to ecological differences that arise from physiographic, vegetational, and climatic differences between the geographically separated sites.

13. Miocene faunas in Jackson Hole show greater affinity with Great Plains faunas with those of the Far West.

14. New Barstovian species include (Cunningham Hill Fauna): *Oreolagus colteri*, new species (ochotonid), *Lignimus transversus*, new species, and *Mojavemys magnumarcus*, new species (geomyids), as well as a new species of *Cupidinimus* (heteromyid) that is named and described elsewhere. *O. colteri* possesses root bumps on the upper cheek teeth as a primitive feature, but is advanced in the short anteroloph of P³. *L. transversus* is very low crowned, like *L. montis*. *M. magnumarcus* is high crowned and possesses enamel chevrons on upper molars. The most similar species in these respects is *M. lophatus*.

15. New Arikareean species include (Emerald Lake Fauna): *Allomys cristabrevis*, new species (aplodontid), and *Archaeolagus emeraldensis*, new species (leporid). *A. cristabrevis* is slightly more primitive than *A. harkseni* in elongation of internal crests, but otherwise is similar. *A. emeraldensis* most closely resembles *A. ennisianus* in intermediate size and the relatively elongate P₃.

16. The late Barstovian Cunningham Hill Fauna yields the first records of the following taxa in the northern Rocky Mountains: *Petauristodon*, *Diprionomys agrarius*, *Lignimus*, *Mojavemys*, *Copemys kelloggae*, *Schaubeumys*.

17. The Hemingfordian East Pilgrim 5 local fauna extends the range of *Merycochoerus proprius magnus* and *Parahippus tyleri* from the Great Plains into the northern Rocky Mountains.

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CAPTIONS FOR PLATES

Plate I.—Screen-washing localities in the Colter Formation. *Top*: Cunningham Hill, UWBM loc. C0236. Bones weather from small channel. Arrow points to hammer for scale. *Bottom*: Man's left foot on North Pilgrim 2, UWBM loc. C0237. Bones erode from scarp to his left.

Plate II.—Teeth of *Domninoidea* cf. *D. storeri*, *Allomys cristabrevis*, new species, *Diprionomys agrarius*, *Spermophilus* near *S. primitivus*, and *Petauristodon* from Colter Formation. Anterior at top for occlusal views. A, *Domninoidea* cf. *D. storeri*, UWBM 62728, M₃, loc. C0237, occlusal view, stereo pair. B, same as A, lingual view, anterior at left. C, *Allomys cristabrevis*, new species, holotype, AMNH 89727, M₁, UWBM loc. C0241, occlusal view. D, *Diprionomys agrarius*, UWBM 62631, M¹ or M², loc. C0237, occlusal view, stereo pair. E, *D. agrarius*, UWBM 62671, M₁ or M₂, loc. C0237, occlusal view, stereo pair. F, *D. agrarius*, UWBM 62660, P₄, loc. C0237, occlusal view. G, same as D, lingual view, anterior at right. H, same as E, labial view, anterior at right. I, same as F, labial view, anterior at left. J, *Spermophilus* near *S. primitivus*, UWBM 62739, M₁ or M₂, loc. C0237, occlusal view, stereo pair. K, *S.* near *S. primitivus*, UWBM 62741, M₃, loc. C0237, occlusal view, stereo pair. L, *S.* near *S. primitivus*, UWBM 62733, M₁ or M₂, loc. C0237, occlusal view, stereo pair. M, *Petauristodon*, species indeterminate, UWBM 62743, M₃, loc. C0237, occlusal view, stereo pair. Scale bars equal 1 mm.

Plate III.—Teeth of lagomorphs from Colter Formation. A, *Oreolagus colteri*, new species, UWBM 62704, P⁴ or M¹, loc. C0237, occlusal view, stereo pair, labial at top. B, *O. colteri*, new species, holotype, UWBM 62698, P⁴ or M¹, from UWBM loc. C0237, occlusal view, stereo pair, labial at top. C, *O. colteri*, new species, UWBM 62720, P⁴ or M¹, loc. C0237, anterior view, labial at left. D, same as A, labial view, anterior at right. E, same as B, labial view, anterior at right. F, *O. colteri*, new species, UWBM 62693, P³, loc. C0237, occlusal view, stereo pair, labial at top. G, same as C, occlusal view, stereo pair, anterior at left, labial at top. H, *O. colteri*, new species, UWBM 62714, M², loc. C0237, occlusal view, anterior at left. I, *Archaeolagus emeraldensis*, new species, AMNH 89801, P₄–M₂, from UWBM loc. C0241, occlusal view, stereo pair, anterior at top. J, *O. colteri*, new species, UWBM 62697, broken DP₃ (anterior two-thirds), loc. C0237, occlusal view, stereo pair, lingual at top. K, *Archaeolagus emeraldensis*, new species, holotype, P₃, loc. C0241, occlusal view, stereo pair, anterior at top. Scale bars equal 1 mm.

Plate IV.—Teeth of *Cupidinimus* and *Peridiomys* from Colter Formation. Anterior at top for occlusal views. A, *Cupidinimus* sp., UWBM 62798, P₄, loc. C0236, labial view, anterior at left. B, Same as A, occlusal view, stereo pair. C, *C.* sp., UWBM 62807, M₁, loc. C0236, occlusal view, stereo pair. D, *C.* sp., UWBM 62788, P⁴, loc. C0236, occlusal view, stereo pair. E, *C.* sp., UWBM 62806, M¹, loc. C0236, occlusal view, stereo pair. F, *C.* sp., UWBM 62809, M₂, loc. C0236, occlusal view, stereo pair. G, *C.* sp., UWBM 62802, M², loc. C0236, occlusal view, stereo pair. H, same as D, anterior view, labial at right. I, same as C, labial view, anterior at left. J, same as F, labial view, anterior at left. K, same as E, lingual view, anterior at right. L, same as G, lingual view, anterior at left. M, *Peridiomys* sp., UWBM 62664, M₁ or M₂, loc. C0237, labial view, anterior at left. N, same as M, occlusal view. O, *P.* sp., UWBM 62638, M¹ or M², loc. C0236, occlusal view, stereo pair. P, same as O, lingual view, anterior at left.

Plate V.—Teeth of *Lignimus transversus*, new species, from Colter Formation. Anterior at top for occlusal views. A, UWBM 62655, P₄, loc. C0237, labial view, anterior at left. B, same as A, occlusal view, stereo pair. C, UWBM 62662, holotype, M₁, loc. C0237, occlusal view, stereo pair. D, UWBM 62663, M₁, loc. C0237, occlusal view, stereo pair. E, UWBM 62666, M₁ or M₂, loc. C0237, occlusal view, stereo pair. F,

same as D, labial view, anterior at right. G, same as C, labial view, anterior at right. H, same as E, labial view, anterior at right. I, UWBM 62687, M₃, loc. C0237, labial view, anterior at right. J, same as I, occlusal view. K, UWBM 62759, P⁴, loc. C0236, occlusal view. L, same as K, anterior view, labial at left. M, UWBM 62777, M¹, loc. C0236, occlusal view, stereo pair. N, same as M, lingual view, anterior at right. O, UWBM 62616, P⁴, loc. C0237, occlusal view. P, same as O, anterior view, labial at right. Q, UWBM 62634, M¹ or M², loc. C0237, occlusal view, stereo pair. R, same as Q, lingual view, anterior at right. S, UWBM 62645, M³, loc. C0237, occlusal view. T, same as S, lingual view, anterior at right. U, UWBM 62621, M¹ or M², from loc. C0237, lingual view, anterior at right. V, same as U, occlusal view.

Plate VI.—Teeth of *Mojavemys magnumarcus*, new species, from Colter Formation. Anterior at top for occlusal views. A, UWBM 62795, P₄, loc. C0236, occlusal view, stereo pair. B, UWBM 62780, M₁, loc. C0236, occlusal view. C, same as A, labial view, anterior at right. D, UWBM 62766, M₂, loc. C0236, occlusal view, stereo pair. E, KUVV 17493, M₃, loc. C0236, occlusal view, stereo pair. F, same as B, labial view, anterior at left. G, UWBM 62784, M₁, loc. C0236, occlusal view. H, UWBM 62783, M₂, loc. C0236, occlusal view, stereo pair. I, UWBM 62770, M₁, loc. C0236, occlusal view. J, same as D, labial view, anterior at left. K, same as G, labial view, anterior at left. L, same as H, labial view, anterior at right. M, same as I, labial view, anterior at right. N, same as E, labial view, anterior at left. O, UWBM 62617, P⁴, loc. C0237, occlusal view, stereo pair. P, same as O, anterior view, labial at left. Q, UWBM 62641, holotype, M¹ or M², loc. C0237, occlusal view. R, KUVV 17498, M³, loc. C0236, occlusal view, stereo pair. S, same as R, lingual view, anterior at right. T, same as Q, lingual view, anterior at right.

Plate VII.—Teeth of *Copemys kelloggae*, *Pseudotheridomys* cf. *P. pagei*, *Parahippus tyleri*, and *Merychippus* from Colter Formation. A, *Copemys kelloggae*, UWBM 62821, M¹–M³, loc. C0236, occlusal view, stereo pair, anterior at top. B, *C. kelloggae*, UWBM 62819, M₁, loc. C0236, occlusal view, stereo pair, anterior at top. C, *Pseudotheridomys* cf. *P. pagei*, KUVV 17486, P⁴ or M¹, loc. C0236, occlusal view, stereo pair, anterior at top. D, *Parahippus tyleri*, CMNH 21617b, P₃–M₃, loc. C0240, occlusal view, anterior at left. E, *Merychippus*, species indeterminate, KUVV 40359c, lower P or M, loc. C0236, occlusal view, anterior at right. F, same as D, labial view. G, same as E, labial view. H, *Parahippus tyleri*, CMNH 21617a, upper cheek teeth, loc. C0240, occlusal view, anterior at left. I, same as H, labial view, anterior at left. Upper scale is for A–C; lower scale for D–G.

Plate VIII.—Oreodonts from Colter Formation. A, *Merychyus arenarum*, UWBM 63261, partial skull, loc. C0239, right lateral view, anterior at right. B, *Merychoerus proprius magnus*, USNM 17919, anterior part of rostrum, loc. C0240, left lateral view, anterior at left. Diagrams at right show the dimensions measured for Tables 15, 17. Abbreviations: C, canine. I, incisor. IF, infraorbital canal. PM, premaxillary suture. PR, dorsal protrusion of premaxillary suture. NV, area of nasal vacuity. ROSLEN, rostrum length. Canine not preserved on side of specimen shown in B, but sketched on lower diagram to illustrate dimension C–M. Anterior end point for dimensions ROSLEN, PM at premaxilla–first incisor junction.

Plate IX.—*Desmatochoerus leidyi* from Colter Formation. A, AMNH 89724, skull, loc. C0241, left lateral view, anterior at left. B, same as A, posterior view. C, AMNH 89724, C₁–P₄, occlusal view, anterior at left.

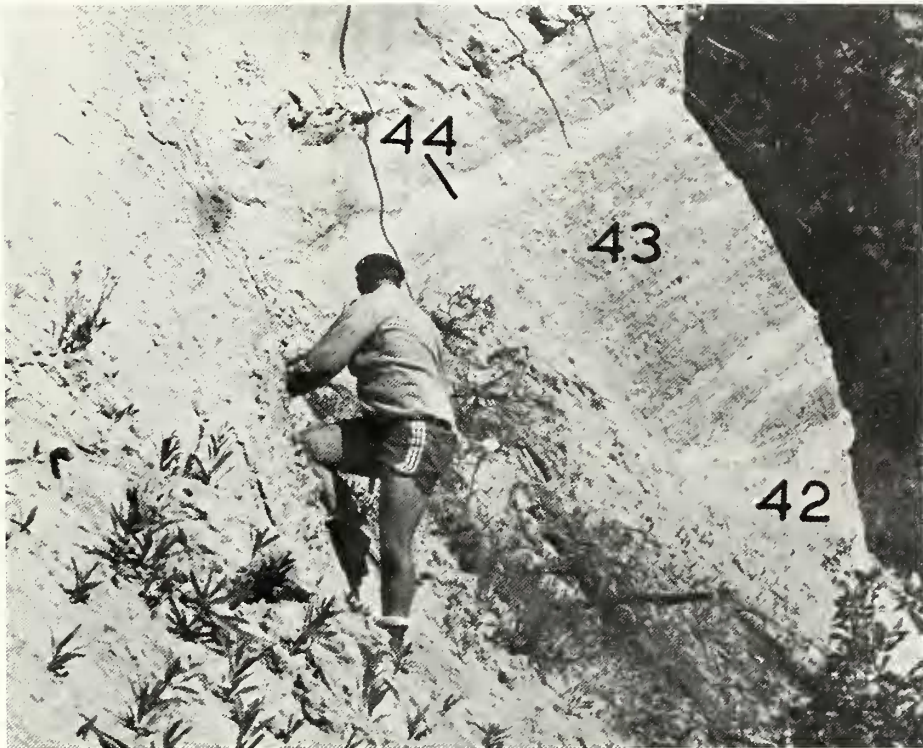


Plate I

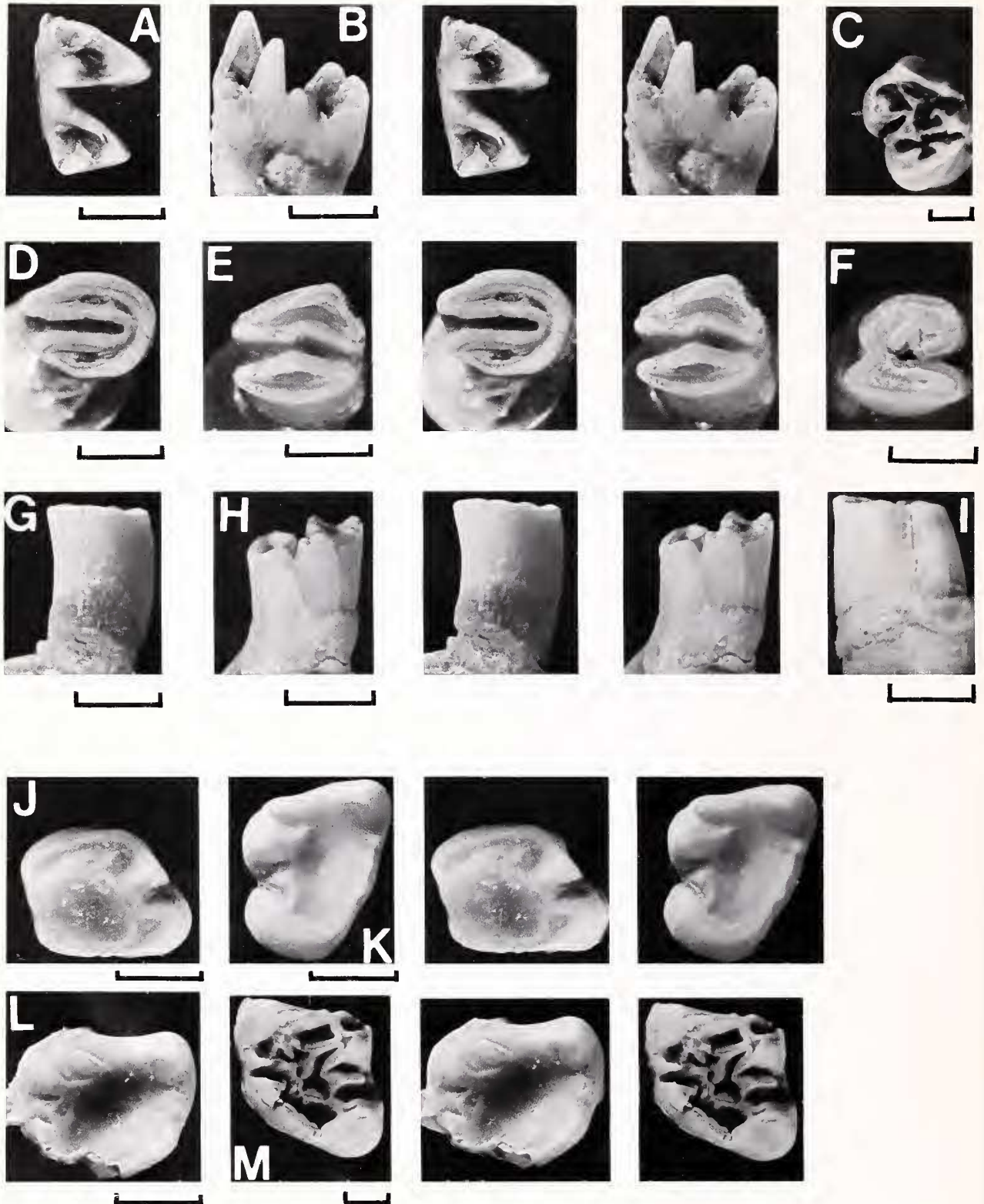


Plate II

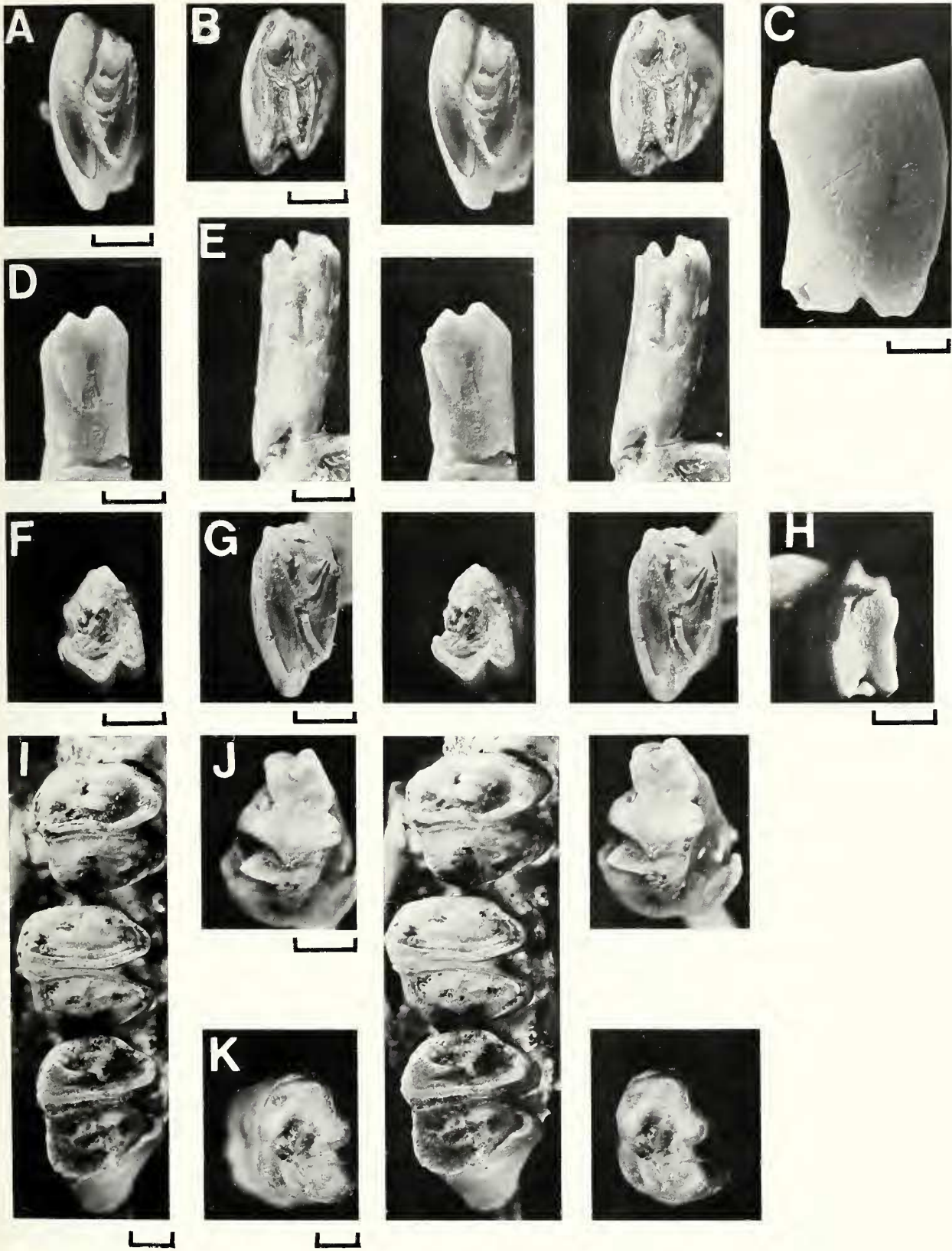


Plate III



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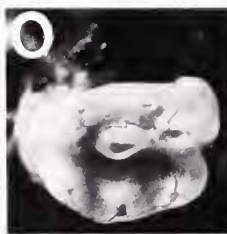


Plate IV

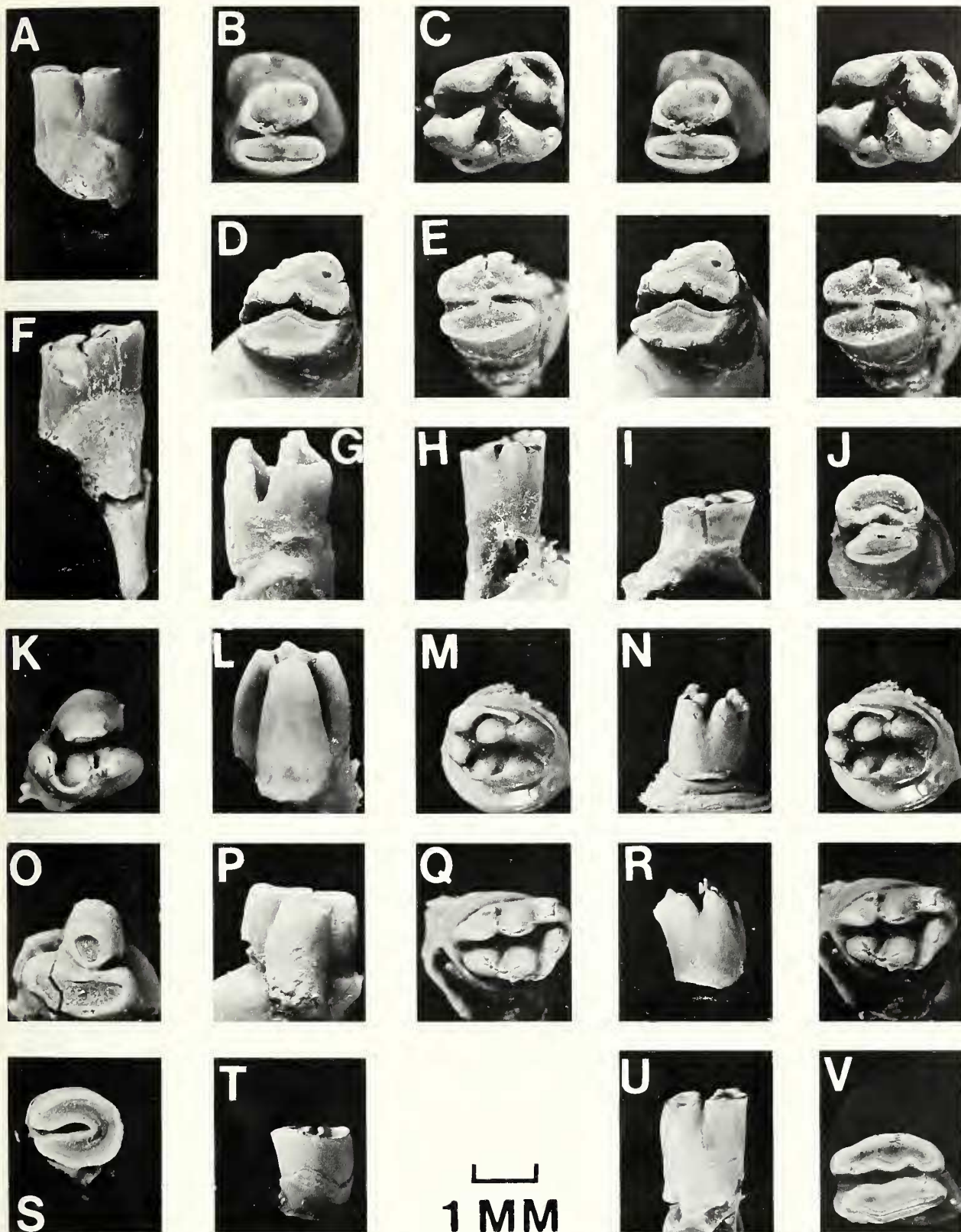


Plate V

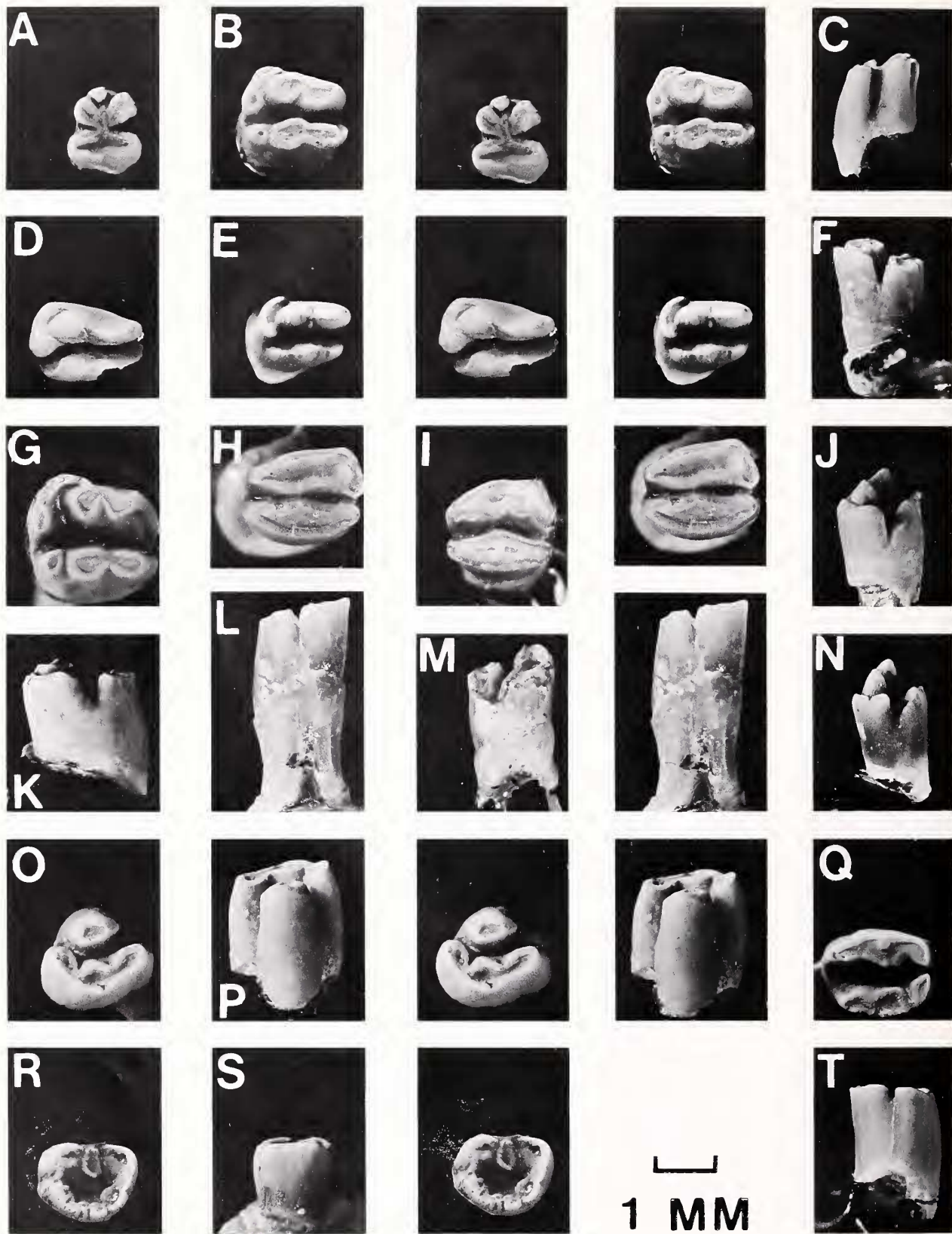
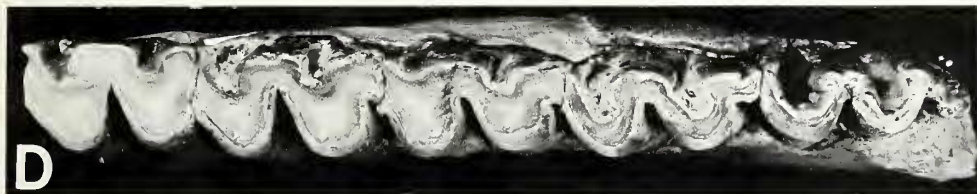
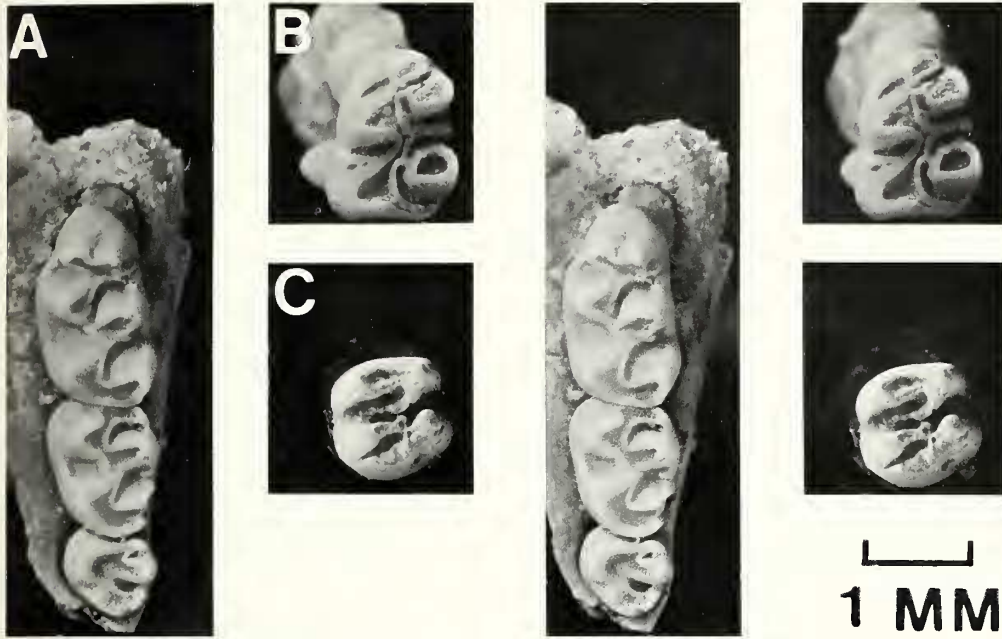
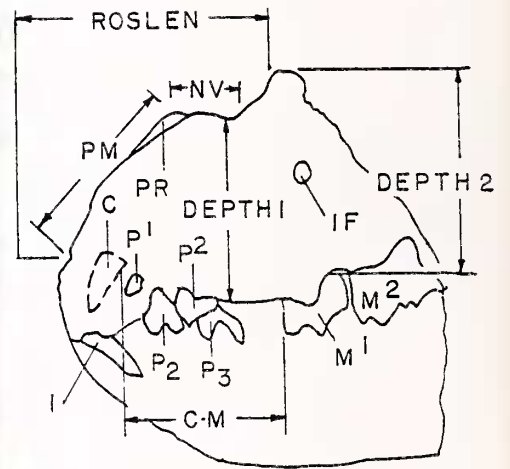
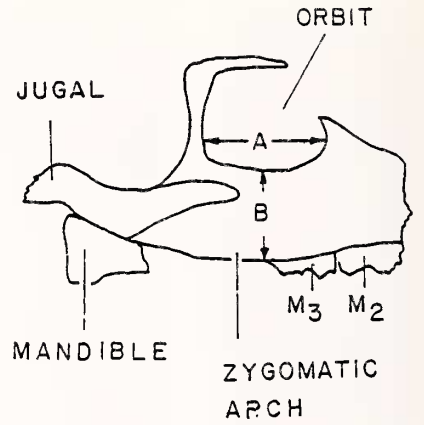


Plate VI



1 CM

Plate VII



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1 CM

Plate VIII

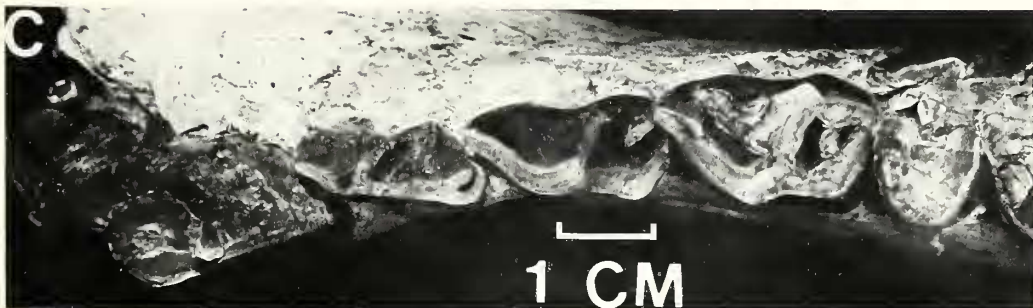
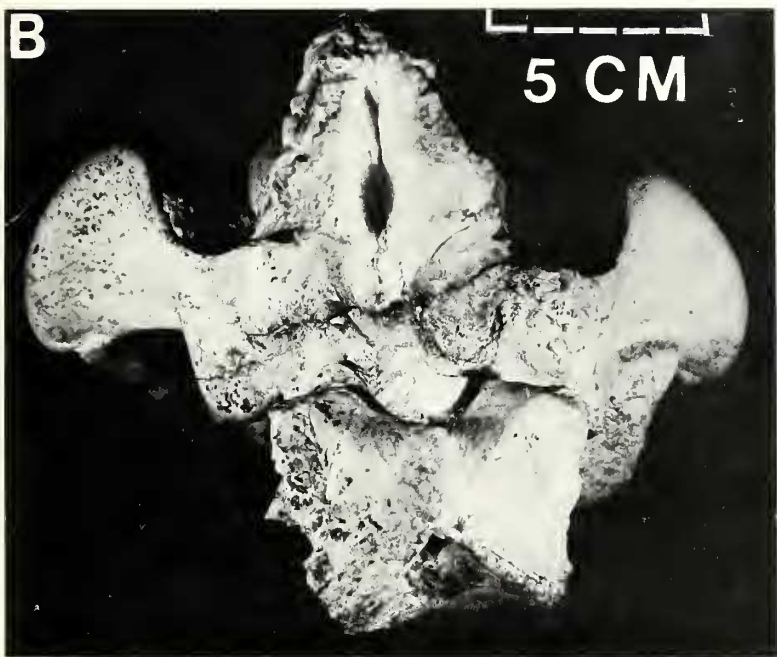


Plate IX